学位申請論文

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主論文

A thesis submitted to the Faculty of Science, Kyoto University in partial fulfillment of the requirements for the degree of Doctor of Science,

THE ROLES OF FLUVIAL GEOMORPHOLOGY IN THE TROPHIC FLOW FROM STREAM TO FOREST ECOSYSTEMS

（河川から森林への栄養移流における河川地形の役割）

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CONTENTS

CHAPTER 1
GENERAL INTRODUCTION

An intermixture of heterogeneous habitats has long been considered to have strong impacts on the community structure and population dynamics in ecological landscapes (Turner 1989, Forman 1995). One of the major ecological processes that operate in such complex mosaics is the interaction between spatial elements, that is, flows of energy and materials and movements of organisms among distinct habitats (Turner 1989, Forman 1995). Conceptual and theoretical studies have argued that the physical layout (referred to as *landscape physiognomy*) and relative amount (*landscape composition*) of habitats contained within the landscape can control the cross-habitat transfers of trophic components, the effects often spreading to surrounding communities (Wiens et al. 1985, Stamps et al. 1987, Dunning et al. 1992).

In natural systems as well, several studies have identified that the physical layout of habitats in a landscape can predict the trophic flow rate, such as movements of detritus (Gasith and Hasler 1976), plants (Hardt and Forman 1989) or animals (Bach 1984) across habitat boundaries (see reviews by Dunning et al. 1992, Polis et al. 1997). The strongest evidence has come from a study on a landscape composed of ocean and island systems. Polis and Hurd (1996) revealed that island size and perimeter largely controlled the rate of detritus input from a productive ocean onto arid islands, with much greater inputs occurring on islands with higher perimeter-area ratios. In addition, such an energy flux subsidizes arthropod detritivores and influences higher trophic levels (e.g., spiders) via island food webs. Thus, island morphology is a major determinant of the biomass and composition of the island animal communities (Polis and Hurd 1996). Polis et al. (1997) argued that such geomorphic effects on trophic linkages are likely ubiquitous and exert critical influences on community maintenance in a variety of spatially heterogeneous landscapes.

Riparian zone, which is a zone of contact between terrestrial and stream ecosystems, has been recognized to be permeable with respect to reciprocal energy and nutrient fluxes (Power and Rainey 2000, Nakano and Murakami 2001, Wiens 2002). For example, many headwater stream ecosystems have a ratio of community production to respiration well below one, indicating

community-wide dependence upon energy from external habitats (e.g., Fisher and Likens 1973, Minshall et al. 1983, Edwards and Meyer 1987). Substantial amounts of terrestrially derived organic matter are pulled downstream by gravity and sustain community metabolism in streams draining forested catchments (Vannote et al. 1980, Wallace et al. 1997, Hall et al. 2000). In contrast, mobile organisms that use both stream and forest ecosystems during ontogeny (e.g., aquatic insects) can convey stream production to the neighboring forests. This lateral transport of stream production often become critical to the maintenance of terrestrial predators (e.g., birds, bats, spiders, and lizards), especially in highly seasonal environments (Jackson and Fisher 1986, Keast 1990, Power and Rainey 2000, Nakano and Murakami 2001). Nakano and Murakami (2001) found that forest birds in a temperate broad-leaved deciduous forest, in which terrestrial arthropod prey was available only for 4-5 months (during the leafing period) of the year, were strongly dependent upon emerging aquatic insects during the leafless period (see also Iwata et al. *in press* a). They estimated that the contribution of aquatic prey reached 25.6% of the annual total energy input to the riparian bird community. Therefore, forest and stream communities are thought to be interdependent upon one another through the interactive exchange of organic materials across their common boundary. However, despite the potential significance for community maintenance, the degree to which forest-stream landscape structure alters such trophic linkages remains poorly understood (Power and Rainey 2000, Wiens 2002, Iwata et al. *in press* a).

A stream system within a drainage basin can be defined as a hierarchically organized geomorphic system across a wide range of scales from entire drainage network (approximate linear scale in second to third order stream: $>10^3$m) to microhabitats (10^{-1}m) (Frissell et al. 1986, Church 2002). At each level in the hierarchy, great heterogeneity exists in fluvial geomorphology that forms the distinctive landscapes of forest-stream ecosystem complex (Fig. 1.1) (Frissell et al. 1986, Pringle et al. 1988, Bisson and Montgomery 1996). The broadest system is a drainage network that includes all surface water in a drainage basin. As water runs off the land, it collects into stream channels which combine in a treelike network. Functionally, a drainage network routes the major conduit of energy, nutrients, and other materials downstream within the drainage basin (Newbold 1992, Fisher et al. 1998, Wiens 2002). Moreover, it may function as energy artery that delivers stream production to terrestrial predators (via aquatic insect emergence) in various habitats. The possibility implies that the development of drainage network structure may

affect the magnitude of aquatic insect flux from stream to terrestrial ecosystems, which in turn may be responsible for determining the distribution and abundance of predators in the drainage basin.

Stream reaches (10^2-10^1m) and channel geomorphic units (10^0m) are hierarchically nested subdivisions, which can be recognized at intermediate hierarchical levels of a drainage network (Fig. 1.1) (Frissel et al. 1986). Stream reaches consist of relatively homogeneous associations of topographic features and include multiple channel geomorphic units (Bisson and Montgomery 1996). Apart from high gradient streams (> 2%), the channel shape of stream reaches is often sinuous and contains a predictable sequence of pools and riffles (Bisson and Montgomery 1996). Stream channels delineate the forest-stream boundary form, so that channel meandering may facilitate the aquatic prey transfer from streams to forests by increasing the stream edges, as in the case of ocean-island landscapes (Polis and Hurd 1996). Channel geomorphic units are relatively homogenous areas of the channel that differ in depth, velocity, and substrate characteristics from adjoining areas (Fig. 1.1) (Bisson and Montgomery 1996). The most generally used channel unit terms for small to mid-sized streams are riffles and pools, which have been described as a fundamental unit for understanding the ecological processes that influence the distribution and abundance of stream biota (Allan 1995, Inoue et al. 1997, McIntosh et al. 2000). Pool is defined as a deep area of slow velocity and fine substrate, created by scour that forms a depression in the streambed or by the impoundment of water upstream from an obstruction to flow (Bisson and Montgomery 1996). The riffle is a distinct topographical hillock area characterized by shallow water, higher velocity and coarser substrate, relative to the adjoining area, at a given discharge. Huryn and Wallace (1987) revealed that nonuniform flow conditions occurring in pools and riffles strongly influenced the distributional pattern of aquatic insect larvae/nymphs (see also Wallace et al. 1995, Maridet et al. 1998). Thus, the spatial arrangement of channel geomorphic units may generate the spatial variation in aquatic insect emergence, which in turn may impact on terrestrial predator distribution.

These possibilities suggest that fluvial geomorphology exert hierarchical controls on terrestrial predator populations in the drainage basin, especially in highly seasonal environments. If it is the case, intensive and extensive hydraulic alterations associated with increasing human activities may exert more strong impacts on the maintenance of terrestrial predators than we expect on the basis of the relatively small areas of stream ecosystems. Therefore, understanding

of the relationships between fluvial geomorphology and terrestrial predator populations is an important prerequisite for developing management plan for watershed biodiversity conservation.

Objectives

In this thesis, I performed field studies to clarify how fluvial geomorphology influenced the distribution and abundance of terrestrial predators by altering the magnitude of aquatic prey flux from streams to forests in temperate forested basins. Specifically, the study was conducted at three hierarchical scales of stream systems, channel geomorphic unit, stream reach, and drainage network, to understand the scale-dependent processes of the stream-forest trophic linkages (Fig. 1.1). In Chapter 2, at channel geomorphic unit scale, I examine the effects of pool-riffle structure on the emergence rate of aquatic insects and the distribution of their predators, riparian web-building spiders. In Chapter 3, at stream reach scale, I investigate how stream meanders influenced the abundances of adult aquatic insects and their predators, insectivorous birds, in riparian forests. In Chapter 4, I examine the effects of stream network structure on the distribution of both aquatic and terrestrial prey and the abundance of forest birds within drainage basins. Finally, in Chapter 5, on the basis of the results obtained, I discuss implications of my research for understanding the issues that arise around watershed biodiversity conservation.

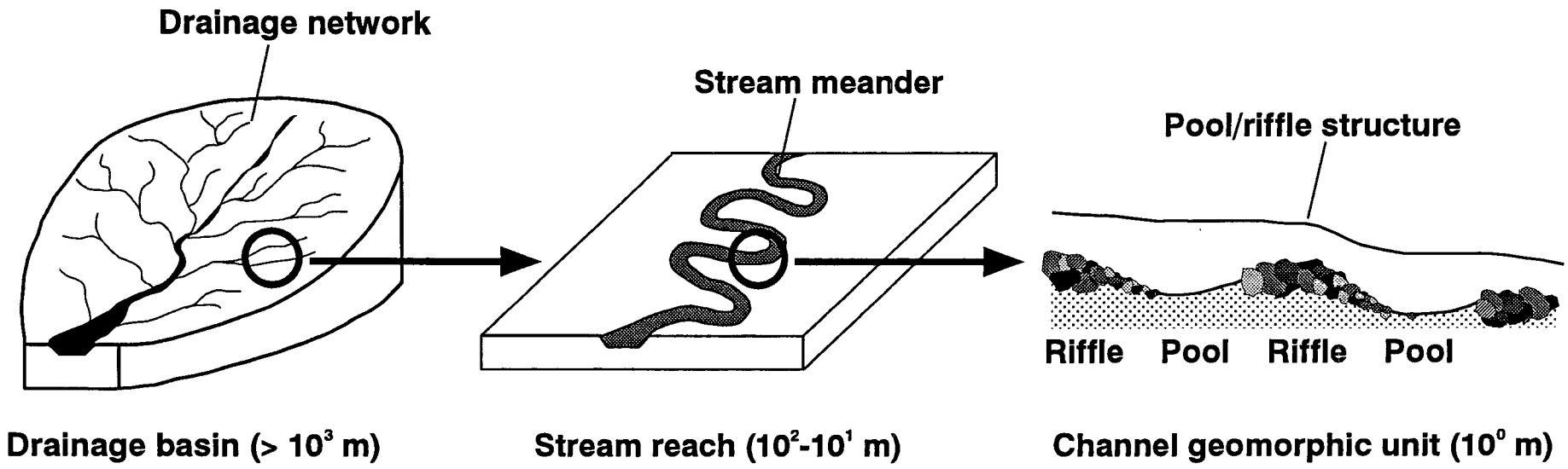


Fig. 1.1 Hierarchical organization of a stream system. Approximate linear spatial scale, appropriate to second- or third-order mountain stream, is indicated in parentheses (see Frissell et al. 1986).

CHAPTER 2

LINKING STREAM HABITATS AND SPIDER DISTRIBUTION: SPATIAL VARIATIONS IN TROPHIC TRANSFER ACROSS A FOREST-STREAM BOUNDARY

In low gradient streams, stream reaches usually exhibit the regular alternations between pools with deep slow water and riffles with shallow fast water (Frissell et al. 1986, Bisson and Montgomery 1996). Such geomorphic and hydraulic habitat characteristics can control the retentiveness of organic matter in the flowing water. For example, pools with slow currents and low transport competence store a large amount of terrestrial detritus, which is the critical resource base of headwater communities (Minshall et al. 1983, Huryn and Wallace 1987). This high retentiveness of pools often enhances the consumption of terrestrial detritus by stream communities (Huryn and Wallace 1987, Wallace et al. 1995, Maridet et al. 1998). Moreover, high localized production in pools associated with abundant detritus has the potential to promote the export of stream production to riparian forests via aquatic insect emergence (see Power and Rainey 2000). In contrast, riffles with high water velocity accumulate less detrital particles, which may prevent the development of detritus-based communities. These possibilities suggest that the emergence rate of aquatic insects is higher in pools than in riffles in headwater streams. Thus, the spatial arrangement of pool and riffle habitats may affect the distribution of riparian generalist predators that utilize both aquatic and terrestrial prey. In this chapter, I examined how pool-riffle structure influenced the distribution of riparian web-building spiders, by comparing pool and riffle habitats in terms of stream and riparian habitat characteristics, abundances of periphyton, detritus, and benthic and emerging aquatic insects, and the diets and density of spiders.

METHODS

Study area

The study was conducted during June and July 2000 in the Horonai Stream and adjacent riparian forest in the Tomakomai Experimental Forest of Hokkaido University (42° 43'N, 141°36'E), southwestern Hokkaido, northernmost island of the Japanese archipelago. The Horonai Stream is

a low gradient, spring-fed stream (8 km^2 in drainage area, gradient < 1%, annual average discharge, 0.24 m^3/s); water temperature remains fairly constant throughout the year, mean daily water temperatures ranging from 7-10 °C in the upper-middle reaches. A study reach (~1 km long) was established in the middle part of the Horonai Stream. The stream channel was sinuous and formed a pool-riffle reach (*sensu* Bisson and Montgomery 1996). Pool was herein defined as a deep area of slow velocity and fine substrate, created by scour that forms a depression in the streambed or by the impoundment of water upstream from an obstruction to flow (see Bisson and Montgomery 1996). The riffle is a distinct topographical hillock area characterized by shallow water, higher velocity and coarser substrate, relative to the adjoining area, at a given discharge. Most of the pools found in the study reach could be classified as lateral scour pools associated with channel meandering, such occurring where the channel encountered the streambank at meander bends (see Bisson et al. 1982). Riffles with moderate turbulence occurred between two lateral scour pools. In the study reach, I selected 20 study channel units (7-20 m length), including 10 pools and 10 riffles, adjacent units being separated by at least 30 m. Habitat characteristics of pool and riffle habitats were described in Table 2.1.

The riparian forest was dominated by deciduous canopy tree species, such as oak (*Quercus crispula* Blume), Japanese maple (*Acer palmatum* var. *matsumurae* Makino), painted maple (*Acer mono* Maxim.), and linden (*Tilia japonica* Simonkai), all of them breaking bud in mid-May and shedding leaves in mid-October. The understory vegetation mainly consisted of lilac (*Syringa reticulata* Hara) and saplings of the above canopy tree species. Over 80% of the entire width of the study reach was covered by forest canopy during the study period.

Periphyton and benthic detritus

The abundances of periphyton and benthic detritus were estimated in pool and riffle habitats. I randomly placed three unglazed ceramic tiles (20 cm x 20 cm area) on the streambed in each channel unit on 6 June (one month prior to the sampling; see Steinman and Lamberti 1996). On 6 July, periphyton grown was harvested from the whole upper surface of each tile and preserved in 1% formalin solution. Benthic particulate organic matter (BOM) accumulated on the streambed was collected using a 225-μm-mesh Surber net sampler (25 x 25 cm quadrat, Miura-Rika, Sapporo) on 5 July. Three samples were randomly collected from the streambed (to 10 cm substrate depth) in each channel unit and immediately preserved in 5% formalin solution. In the

laboratory, subsamples of well-mixed periphyton suspensions were collected on precombusted glass-fiber filters and dried at 60 °C for 48 h. The BOM contained in each Surber net sample was also dried after the removal of all invertebrates. Those samples were weighed to the nearest 0.01 mg, combusted at 550 °C for 3 h and reweighed to obtain ash-free dry mass (AFDM). The AFDM was then averaged for each channel unit (n = 3) to obtain the periphyton and BOM standing crops per unit area of the streambed (AFDM g/m^2).

Aquatic insects

Benthic aquatic insect larvae/nymphs were collected simultaneously with the BOM samples on 5 July (n = 3 for each channel unit; see above). Aquatic insects emerging from the stream were collected from 28 June to 4 July with a square-pyramid emergence trap (1 x 1 m area, 1 m high, made of 500-μm mesh), set 1 cm above the stream surface at a randomly-selected sampling point in each channel unit. Trapped insects were collected after a 2-d deployment and the trap was then moved to another point selected within the channel unit, this procedure being repeated three times during the sampling period.

Aquatic insects in benthos and emergence samples were identified to the lowest recognizable taxon, their damp mass was weighed to the nearest 0.01 mg after blotting for 10 s, and converted into dry mass by multiplying by the taxon-specific damp mass-dry mass ratio (S. Nakano, unpublished data). In this study, invertebrates that spend their whole life span in water (such as Amphipoda, Bivalvia and Oligochaeta) were excluded from the analyses because those invertebrates were not consumed by web-building spiders. Aquatic insects were grouped into three trophic guilds; detritivores, grazers or predators. Insects categorized as gatherers, shredders and filterers in the functional feeding group classification (Merritt and Cummins 1978) were regarded as detritivores, except a gatherer *Baetis thermicus* Uéno, which functions as a grazer (Kuhara et al. 1999). Scrapers and engulfers were regarded as grazers and predators, respectively. The benthic insect biomass in each channel unit was averaged separately for each trophic guild (n = 3) and expressed as the dry mass per unit area of the streambed (mg/m^2). Similarly, the emergence rate of aquatic insects was estimated as the dry mass per unit area per day (mg m^{-2} day^{-1}).

Spider density and diets

The density of web-building spiders was estimated in riparian forests, juxtaposing each pool and riffle habitat, during 22-27 June. A 2-m wide belt transect was established along either side's streambank (randomly chosen) contiguous with the entire length of each study channel unit (10 belt transects for each of pools and riffles). In each belt transect, all web-building spiders found to a maximum height of 2 m were collected during the nighttime (1900–2200 h), when they were most active. In addition, spiders that built their webs on vegetation overhanging the study channel unit (to a 2 m high) were also collected. Concurrently, all arthropods recently entangled in spider webs, in which spiders were present, were collected in order to examine the prey items of web-building spiders. To ensure sufficient sample sizes, additional sampling for spider prey items was also implemented during 1-5 July along the study reach (within 2 m from the shoreline), but avoiding the transects used for estimating spider density.

Spiders collected were identified to species according to Chikuni (1989). Because species belonging to the same family exhibit similar foraging tactics in terms of web architecture and web site selection (Wise 1993), spider species were grouped by family, including Tetragnathidae, Linyphiidae, Araneidae, Theridiidae and Agelenidae. Of those, tetragnathid and linyphiid spiders together accounted for > 80% of the total density of the web-building spider assemblage when all the samples were combined (tetragnathids, 57.9%; linyphiids, 26.5%). Thus, only tetragnathid and linyphiid spiders were included in the analyses. Tetragnathids spin sticky orb webs that are often oriented horizontally, while linyphiids build sheet webs of entirely non-sticky silk, which are basically comprised of a horizontal sheet with scaffolding above and below. Their densities (spiders/m^2) were determined for each sampling area (belt transect and overhanging vegetation cover). For the analyses of prey items, arthropods collected from spider webs were identified, and the dry mass of each item determined as above. For tetragnathid and linyphiid spiders, the percentage of dry mass contributed by each prey item was determined separately for each of the pool and riffle transects.

Riparian habitat measurements

Riparian habitat variables, including stand density and cover area of overhanging vegetation, were measured in each belt transect on 3 July. Riparian stands were grouped into > 2-m tall trees (hereafter mid-overstory) or ≤ 2-m tall shrubs (shrubs). Mid-overstory and shrub densities (stands/m^2) were determined for each belt transect. The area of vegetation cover overhanging the

stream channel, where spider sampling was made, was also measured. The length and width of each cover were measured to obtain the areal proportion of overhanging vegetation cover to the belt-transect area.

Data analyses

All variables were transformed as $\log_{10}$ (x + 1) or $\log_{10}$ (x) for exact values or as arcsin ($p^{0.5}$) for percentage values to standardize variances and improve normality (Zar 1984).

RESULTS

Food resources

The abundance of food resources for aquatic insects differed between pools and riffles (Fig. 2.1). Unpaired *t* tests showed a significant difference in BOM standing crop between channel units (t_{18} = 4.8, $P < 0.001$), with pools having three times more BOM than riffles on average. However, no significant difference was detected for periphyton standing crop between the two channel-unit types (t_{18} = 1.7, P = 0.114).

Benthic biomass of aquatic insects

The biomass of benthic aquatic insects differed significantly between channel units ($F_{1, 54}$ = 4.2, P = 0.046) and among trophic guilds ($F_{2, 54}$ = 148.1, $P < 0.001$; two-way ANOVA, Fig. 2.2). The biomass was 1.8 times greater in pools (1.78 ± 0.20 g/m^2 [mean ± SE]) than in riffles (1.00 ± 0.13 g/m^2; n = 10 for both) when all of the trophic guilds were combined. In both pools and riffles, detritivores accounted for ≥ 70% of the total biomass of the benthic insect assemblages. Two-way ANOVA also showed a significant interaction effect ($F_{2, 54}$ = 19.9, $P < 0.001$), indicating that the effects of channel units differed among the trophic guilds (Fig. 2.2). Unpaired *t* tests showed that pools had a significantly greater detritivore biomass (t_{18} = 3.5, P = 0.003), while riffles had more abundant grazers (t_{18} = -4.1, $P < 0.001$). No significant effects of channel units were, however, detected for predatory insects (t_{18} = 1.6, P = 0.130).

Emergence rate of aquatic insects

The emergence rate of aquatic insects also differed markedly between channel units ($F_{1, 54}$ = 35.5,

$P < 0.001$) and among trophic guilds ($F_{2, 54} = 31.2$, $P < 0.001$; two-way ANOVA, Fig. 2.3). The aquatic insect emergence from pools (11.7 ± 2.0 mg m^{-2} day^{-1} [mean ± SE]) was 4.5 times greater than that from riffles (2.6 ± 0.7 mg m^{-2} day^{-1}; $n = 10$ for both), when all of the trophic guilds were combined. Detritivores accounted for 77 ± 4 % (mean ± SE) of the total emergence from pools, but only 30 ± 8 % ($n = 10$ for both) of the total emergence from riffles. Two-way ANOVA also showed a significant interaction effect ($F_{2, 54} = 18.7$, $P < 0.001$), indicating that the effects of channel units differed among the trophic guilds. According to unpaired t tests, the emergence rate of detritivores was significantly higher in pools than in riffles ($t_{18} = 6.6$, $P < 0.001$), but those of grazers and predators did not differ between the two channel-unit types (grazers, $t_{18} = 1.4$, $P = 0.193$; predators, $t_{18} = 1.1$, $P = 0.297$, Fig. 2.3).

Spider diets and density

Emerging aquatic insects contributed to nearly all of the diets of tetragnathid spiders in the pool (97%) and riffle (99%) transects (Table 2.2). Among aquatic prey, detritivores were a dominant prey item of tetragnathid spiders in both pool and riffle transects. Linyphiid spiders also depended heavily on aquatic prey, which comprised 64% and 61% of their diets in pool and riffle transects, respectively. As for tetragnathids, aquatic detritivores were the most important prey item for linyphiid spiders.

The riparian transects juxtaposing pools had two times higher density of tetragnathid spiders than those adjacent to riffles (pool transect, 1.3 ± 0.6 spiders/m^2 [mean ± SE]; riffle transect, 0.6 ± 0.2 spiders/m^2; $n = 10$ for both), the difference between the transect types being significant (t test; $t_{18} = 3.9$, $P = 0.001$). Simple linear regression analyses revealed that tetragnathid density increased significantly with the emergence rate of aquatic detritivores ($R^2 = 0.39$, $P = 0.003$, $n = 20$, Fig. 2.4). However, that density was not related to the emergence rate of the other guilds or riparian habitat variables ($R^2 = 0.03$-0.10, $P = 0.166$-0.491, $n = 20$ for all). The density of linyphiid spiders also showed a positive relationship with the emergence rate of detritivores ($R^2 = 0.32$, $P = 0.009$, $n = 20$, Fig. 2.4). Nonetheless, linyphiid density did not differ between the transect types (pools, 0.50 ± 0.25 spiders/m^2; riffles, 0.33 ± 0.18 spiders/m^2; t test, $t_{18} = 1.89$, $P = 0.075$). In addition to detritivore emergence, shrub density in the riparian transects significantly influenced linyphiid density ($R^2 = 0.44$, $P = 0.002$, $n = 20$, Fig. 2.4). When the effect of shrub density was statistically controlled, a significant difference was found in linyphiid

density between pool and riffle transects (one-way ANCOVA using shrub density as a covariate, $F_{1, 17} = 6.45$, $P = 0.021$). The other riparian habitat characteristics and emergence rates of grazers and predators had no significant effects on linyphiid spiders, as in the case of tetragnathid spiders ($R^2 = 0.01$-0.14, $P = 0.111$-0.840, $n = 20$ for all).

DISCUSSION

The present study showed that pool-riffle structure strongly influences the distribution of riparian web-building spiders by generating spatial heterogeneity of aquatic insect emergence from the stream. In both riparian habitats contiguous with pools and riffles, tetragnathid and linyphiid spiders relied heavily on emerging aquatic insects, as have been reported in many regions (Yoshida 1989, Williams et al. 1995, Power and Rainey 2000). In particular, the consumption of abundant aquatic detritivores by both spider groups was very high in both pool and riffle transects. Furthermore, simple regression analyses revealed that variation in detritivore emergence was the factor most strongly implicated in the density of tetragnathid spiders (Fig. 2.4). Because pools exported a much greater biomass of aquatic detritivores than did riffles (Fig. 2.3), tetragnathid spiders aggregated in the riparian habitats adjacent to pools, attaining a density approximately twice that in habitats adjacent to riffles. The difference in linyphiid density between pool and riffle transects was less clear, however, even though their density was also associated with the emergence rate of detritivores. Unlike the tetragnathid two-dimensional orb webs, linyphiid spiders build structurally complex, three-dimensional sheet webs, requiring a triangular fork and overhanging projection to support the main sheet of silk and vertical trapping threads (Janetos 1982). In fact, linyphiid density was also positively related to the density of shrubs, the dense branches of which can supply the support necessary for sheet webs. In addition, linyphiid density normalized by shrub density differed significantly between pool and riffle transects. Thus, limitations of the riparian habitat structure related to specific web sites are considered a cause to prevent the aggregation of linyphiid spiders in the habitats adjacent to pools (see Janetos 1982, Rypstra 1983).

The relatively high emergence rate of aquatic detritivores in pools seems to be in large part attributable to the greater amounts of detritus and resultant greater biomass of benthic detritivores in pools than in riffles. The low transport competence of pools, associated with slow

currents, may have resulted in the deposition of fluvial organic matter (Naiman and Sedell 1979, Huryn and Wallace 1987). In fact, BOM standing crop was negatively related to mean current velocity in each channel unit (R^2 = 0.53, P < 0.001, n = 20). This high degree of pool retentiveness for detrital particles increases the biomass of benthic aquatic insects. This was also supported by simple linear regression analyses, which showed that benthic detritivore biomass was positively related to BOM standing crop (R^2 = 0.51, P < 0.001), as well as negatively to current velocity (R^2 = 0.49, P < 0.001, n = 20 for both). Furthermore, the total benthic biomass in pools was also greater than that in riffles, because detritivores overwhelmingly predominated in the aquatic insect assemblages.

Terrestrially derived organic materials and detritivorous insects are the key components driving reciprocal trophic exchanges at the interface between the forest and stream ecosystems. The assemblage structures predominated by detritivorous insects in both pools and riffles reflect the primary role of detrital resources in forming the trophic base of aquatic insect assemblages (Vannote et al. 1980). In the Horonai Stream, the observed BOM dynamics (Kishi et al. 1999, Shibata et al. 2001), together with its stable carbon isotope ratio close to that of riparian leaf litters (C. Kato, T. Iwata and E. Wada, unpublished data), indicate that a large fraction of detritus originates from heavy autumnal leaf falls. Thus, aquatic insect assemblages appear to be maintained primarily by a linkage between the forest and stream ecosystems, via allochthonous inputs of detritus from the surrounding forests or from upstream areas (see Wallace et al. 1997, Hall et al. 2000, Finlay 2001). More importantly, the present findings indicate that via the emergence of aquatic detritivores, terrestrial detritus may support riparian generalist predators after having been assimilated into organic tissues by stream food webs. Stream ecosystems have long been regarded as a 'sink' for terrestrial products, because terrestrial detritus once entered streams has been considered as being either transported downstream or broken down by biological uptake or physical-chemical processes (Fisher and Likens 1973, Webster et al. 1995). However, streams should no longer be viewed only as recipient systems, but also as systems that return terrestrially derived organic matter back to riparian food webs by converting it into resources available for terrestrial predators. Pool habitats play a significant role in this organic matter dynamic across the boundary between forest and stream ecosystems (as schematized in Fig. 2.5). They prolong the retention of terrestrial detritus in flowing water, thereby forming localized productive areas of aquatic insect assemblages (Bilby and Likens 1980, Minshall et al.

1983, Huryn and Wallace 1987). As a result, pools function as a major conduit for organic matter exports from the stream to the terrestrial environment, supporting high population density of riparian generalist predators.

Table 2.1. Means and SDs of six stream habitat variables in pool and riffle habitats (n = 10 in each).

Variable	Pool	Riffle
Wetted width (m)	3.9 ± 0.5	4.2 ± 0.6
Depth (cm)	33 ± 4	17 ± 3
Current velocity (cm/s)	21 ± 3	37 ± 4
Sand (%)	35 ± 18	17 ± 13
Gravel (%)	51 ± 10	55 ± 18
Pebble (%)	14 ± 10	28 ± 15

Note: Each habitat variable was measured according to Iwata et al. (2003) and Iwata et al. (*in press* b).

Table 2.2. Diet compositions (% in dry mass) of tetragnathid and linyphiid spiders in two riparian habitats adjacent to pools and riffles. Total numbers of prey collected given in parenthesis for each category.

		Prey category				
Spider	Habitat	AD	AG	AP	AU	TA
Tetragnathids	Pool	89.3 (164)	0.3 (3)	7.0 (17)	0.4 (1)	3.0 (13)
	Riffle	95.1 (82)	1.7 (5)	1.8 (13)	0.7 (1)	0.7 (7)
Linyphiids	Pool	50.2 (31)	2.0 (3)	11.8 (10)	0.0 (0)	36.0 (21)
	Riffle	45.4 (28)	3.9 (2)	8.7 (5)	2.5 (2)	39.5 (14)

Note: Abbreviations: AD, aquatic detritivores; AG, aquatic grazers; AP, aquatic predators; AU, aquatic unknown; TA, terrestrial arthropods.

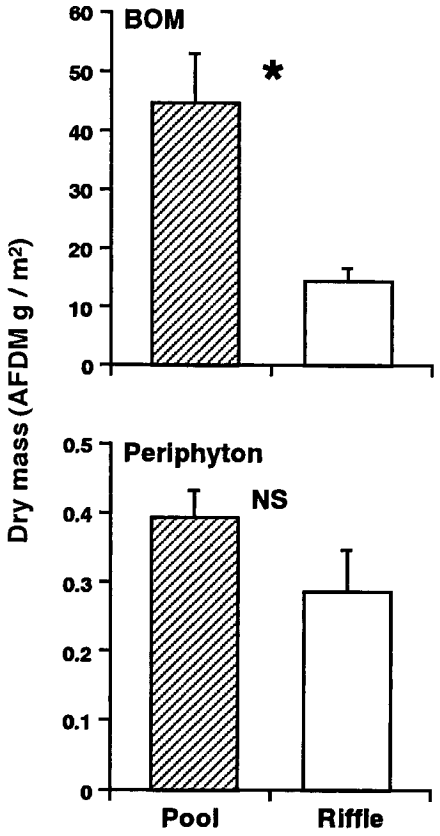


Fig. 2.1. Standing crops (mean ± 1 SE ash-free dry mass g/m^2; n = 10) of benthic organic matter (BOM) and periphyton in pool and riffle habitats. Asterisk denotes significant difference based on t test between pools and riffles.

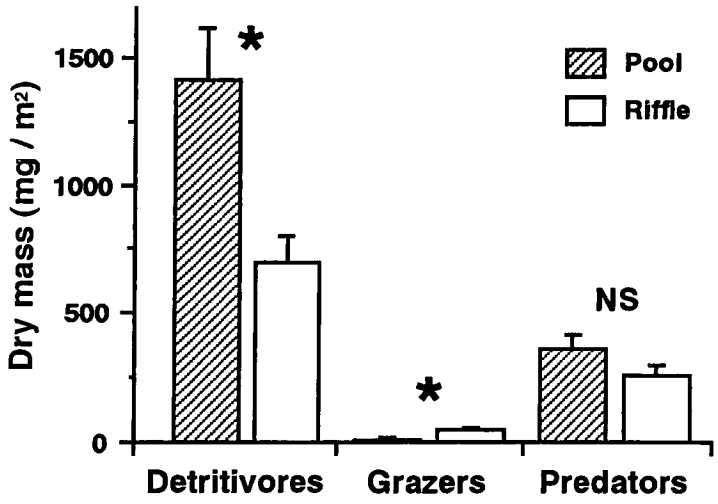


Fig. 2.2. Benthic biomass (mean ± 1 SE mg/m^2; n = 10) of aquatic detritivores, grazers and predators in pool and riffle habitats. Shaded and blank bars denote pools and riffles, respectively. Asterisks denote significant differences based on t tests between pools and riffles.

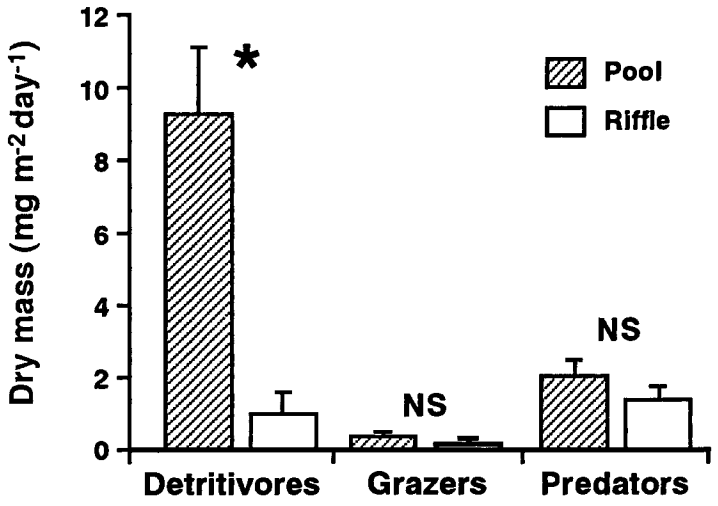


Fig. 2.3. Emergence rate (mean ± 1 SE mg m^{-2} day^{-1}; n = 10) of aquatic detritivores, grazers and predators in pool and riffle habitats. Shaded and blank bars denote pools and riffles, respectively. Asterisk denotes significant difference based on t test between pools and riffles.

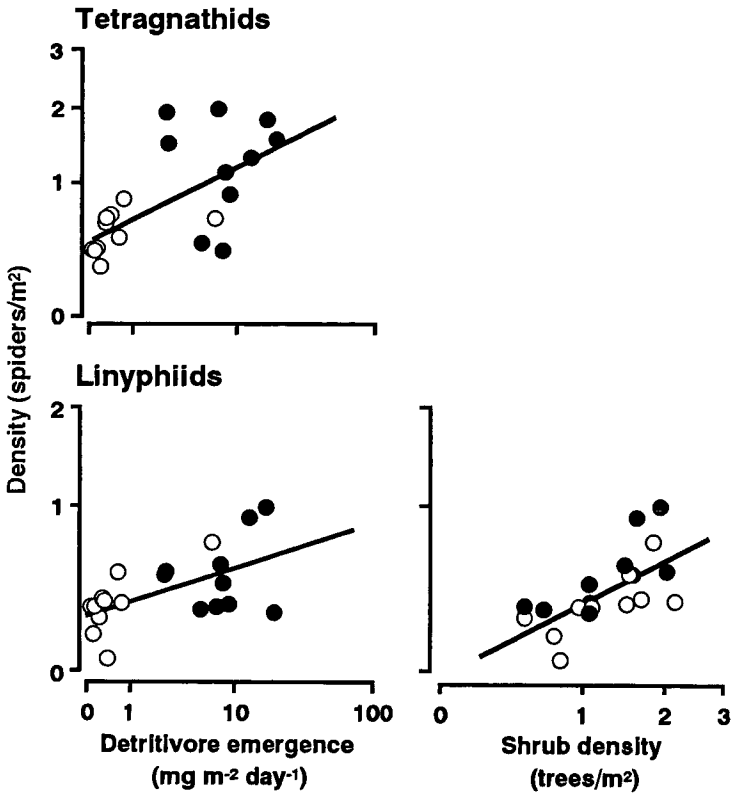


Fig. 2.4. Relationships of spider density (tetragnathids and linyphiids) with riparian habitat variables and aquatic insect emergence in 20 study channel units. Significant relationships only are presented, with regression lines (see text). Solid and open circles indicate pools and riffles, respectively. All axes are logarithmic scale.

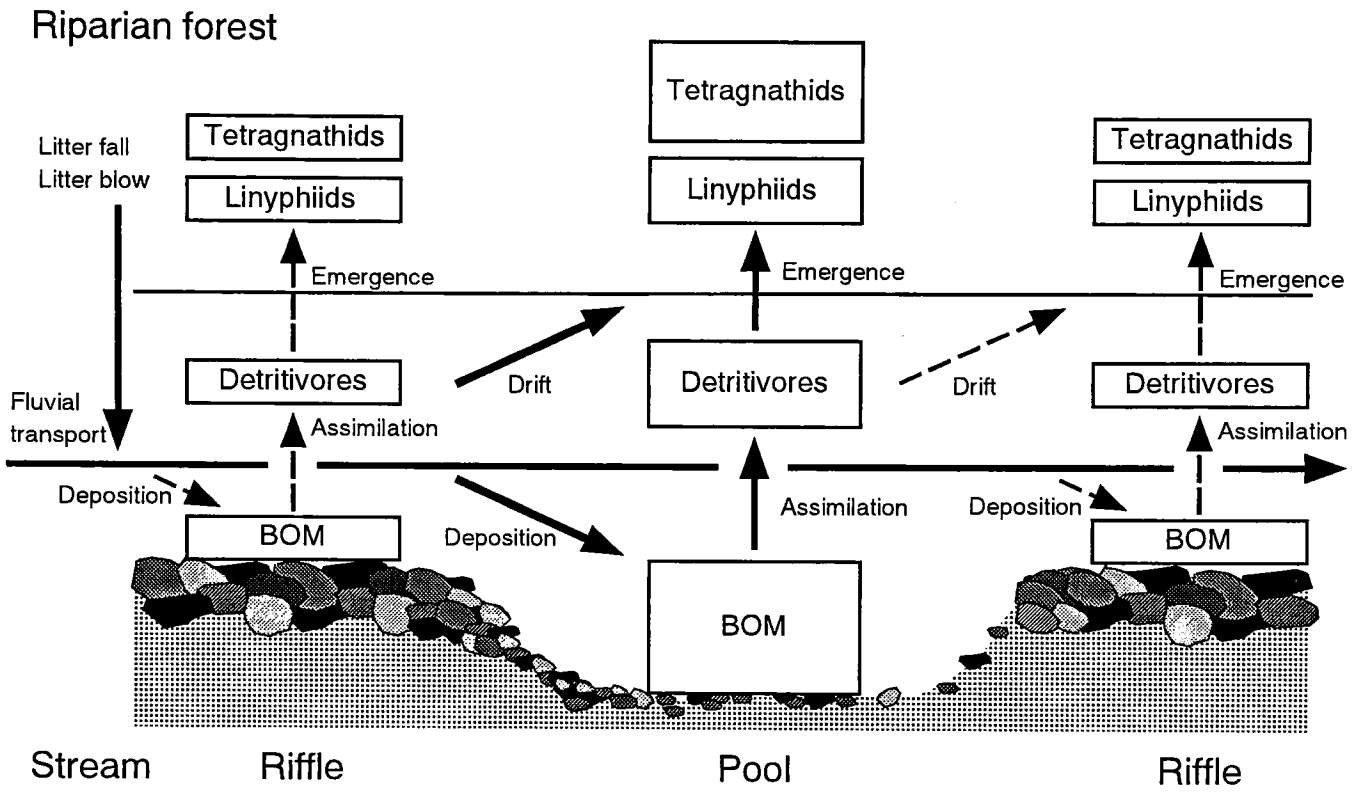


Fig. 2.5. A simplified diagram of the major components of organic flow across the boundary between a pool-riffle reach of the Horonai Stream and surrounding forest. Solid arrows indicate possible important pathways predicted by the present study.

CHAPTER 3
STREAM MEANDERS INCREASE INSECTIVOROUS BIRD ABUNDANCE IN RIPARIAN DECIDUOUS FORESTS

In the previous chapter, I illustrated the importance of the spatial arrangement of channel geomorphic unit (i.e., pool-riffle structure) in determining the distribution of riparian terrestrial predators. In this chapter, I document such ecological effects of stream geomorphology at broader scale. Stream reach is the scale at which sequences of pools and riffles are nested, and channel meandering can be distinguished as the most typical geomorphic feature in low gradient streams (Frissell et al. 1986). Because the shape of habitat boundary is a landscape feature that controls the rate of cross-habitat trophic transfers (Gasith and Hasler 1976, Stamps et al. 1987, Dunning et al. 1992, Polis et al. 1997), stream meanders can impact strongly on riparian generalist predators by altering the magnitude of aquatic prey transfer from streams to forests. In this chapter, I examined the hypothesis that landscapes including more highly sinuous streams would have a greater supply of emerging aquatic insects per unit area of forest and therefore sustain greater insectivorous bird abundance. This study was conducted during spring period (before the riparian forests were leafed out), when terrestrial prey abundance is low. In this season, many insectivorous birds strongly depend upon emerging aquatic insects in temperate riparian deciduous forests (Keast 1990, Nakano and Murakami 2001).

METHODS

Study area

The study was conducted in riparian deciduous forests of eight streams, discharging into the Pacific Ocean through Tomakomai City (42°38'N, 141°36'E), southwestern Hokkaido, Japan (Fig. 3.1). These low gradient (≤ 1%), cold-spring-fed streams are highly sinuous and have no fringing floodplains, instead having well-developed forests along the edges of the active stream channels. The forest type was homogeneous across the drainage basins, mainly comprising second-growth deciduous forest that had developed after an eruption of Mt Tarumai in 1739.

Bird and insect sampling were made from 10 May to 10 June 2000 in 26 study plots (100 m long x 50 m wide), established along headwater reaches (first- or second-order, 15-80 m in altitude) of the eight streams (Fig. 3.1). The study plots included a variety of stream geomorphological types, in terms of channel sinuosity and width. The two end points of the centerline (100 m long axis) of each study plot were set on the stream channel, and the stream channel between the points was all included within the plot. Sampling was initiated after confirmation of the arrival of most summer migrants (in early May) and completed before the riparian trees had fully developed their leaves (from mid to late June). Further information on the site description was given elsewhere (Iwata et al. *in press* a).

Stream geomorphology and riparian forest measurements

The planform geometry of the study reach in each plot was measured with a compass and measuring tape, and the area, length (along the channel axis, hereafter stream length) and mean wetted width (stream width) of the study reach within each plot were determined. The riparian forest condition in each study plot was surveyed using a transect method. Four equally spaced transects of 4 m width were established from the stream edge to the margin of each study plot. The transects were set alternately on the left- and right-hand banks of the stream channel. The diameter at breast height (dbh) of all living trees ≥ 3 cm and snags (standing dead trees) ≥ 10 cm in dbh in each transect was measured to the nearest 1 cm. The density (trees/m^2) and mean dbh (cm) were then calculated separately for live trees and snags from the data obtained from the four transects in each study plot.

Insect sampling and analyses

The distribution of adult aquatic insects and terrestrial aerial insects in the riparian forest as a function of stream proximity were surveyed by Malaise-trap sampling (Townes 1972). Half-sized Malaise traps (1 m high, 1 m long, 0.6 m wide, made of 0.5 mm mesh) were deployed concurrently in two study plots of the Uenae and Horonai streams, both having relatively straight channels. In each plot, the traps were placed along a transect at distances of 0 (over stream), 1, 2, 5, 10, 15, 30, and 60 m at a right angle to the active stream channel (30 cm above stream surface or ground), and operated for two six-day sessions within the sampling period (10-16 May and 16-22 May). The insects collected were preserved in 70% ethanol, sorted into aquatic and terrestrial

aerial insects in the laboratory, and their dry mass were determined as described in Chapter 2 (page 8). The abundance of emerging aquatic insects and terrestrial aerial insects at each established point was then expressed as dry mass per trap per day (mg $trap^{-1}$ day^{-1}).

The Malaise-trap sampling was also conducted in order to estimate food availability for the insectivorous birds in each study plot. Eight 25-m square grids were established in each study plot. A Malaise trap was placed for four or five days at the center of a single grid, which was randomly chosen from the eight grids. Such a procedure was repeated six times during the study, avoiding use of the same grid during different sampling periods. Insect biomass in Malaise trap placed close to the ground is known to be a useful indicator of food availability for forest insectivorous birds (Johnson and Sherry 2001). Trapped insects were examined as above and the mean of dry mass per trap per day (mg $trap^{-1}$ day^{-1}, n = 6) was used to express the abundance of both adult aquatic insects and terrestrial aerial insects in each plot.

In addition, the emergence of aquatic insects from the study reach was estimated in each study plot. Because the emergence rate is known to differ greatly between channel unit types (Power and Rainey 2000, Chapter 2), sampling was made separately for pools and glides. Three channel-units were randomly chosen from each of the pools and glides. In each individual channel-unit chosen, emerging aquatic insects were collected with a emergence trap (see Chapter 2) set at 1 cm height above the stream surface. The trap was deployed for four or five days and subsequently moved to another selected channel-unit. The emergence rate of aquatic insects was then determined as dry mass per unit area per day (mg m^{-2} day^{-1}), and was averaged separately for pools and glides (n = 3 for each). The mean emergence of each channel-unit type (pools and glides) was multiplied by the areal proportion of each channel-unit type and summed for each study reach, so as to obtain an estimate of the reach-based, habitat-weighted emergence rate of aquatic insects (mg m^{-2} day^{-1}; hereafter local emergence).

Bird observation

Bird abundance in each study plot was surveyed on every day not affected by rain, fog or strong wind during the sampling period. All study plots were visited at intervals of five or six days, and censused twice in each of the early morning (0500-0800 h), late morning (0800-1100 h) and late afternoon (1430-1730 h) periods, producing a total of six observations per plot during the sampling period. An observer walked over the entire area of each study plot, following the grid

on a systematic basis, all birds seen or heard within the plot being recorded during a 1-h observation period. I attempted to record each individual only once during each observation. Birds that flew over a plot without landing were not included in the data for that plot.

Foraging behavior was also recorded during each observation. When a single foraging bird was encountered, prey attacks (within a 3-min period) were recorded unless other birds were detected. For each prey attack, foraging space and prey item (if seen) were recorded. Identification of prey items (especially tiny arthropods), however, was often difficult. Therefore, after observing the foraging behavior of each individual bird, the observer carefully checked the foraging substrate for any remaining prey or swarm (whenever possible) in the area in which the bird had concentrated its attacks. In the analyses of these foraging records, I used only the first sighting of prey attacks of an individual so as to better satisfy the independence between the records.

A total of 42 species of forest birds was observed during the study, comprising 17 species of year-round residents and 25 species of summer breeding migrants. Of those, 31 species were regarded as insectivorous and were examined in the study (Table 3.1). All insectivorous birds observed were classified into three foraging guilds, flycatchers, gleaners or bark probers, based on the morphological features that reflect their specific feeding habits (Table 3.1, see Iwata et al. *in press* a for details of the guild classification). Flycatchers (Muscicapinae) usually sally out from a perch, capture an arthropod (usually flying insects) and return to the perch. Bark probers, including woodpeckers, nuthatch and treecreepers, usually peck or probe the bark. Gleaners, including the other species of Passeriformes observed and oriental cuckoo, often search leaves, buds, branches or ground for prey (usually stationary arthropods), gleaning them from those substrates, although their feeding habits become occasionally flexible depending on the kind of food available. The abundance of each guild in the study plot (birds/plot) was determined by averaging the number of individuals detected over the six observations.

Data analyses

The foraging spaces used by birds were examined in terms of distance from the stream channel. Each of the study plots was divided into six parts, 0 (active stream channel), 0-5, 5-10, 10-15, 15-30 and $\geq$ 30 m from the stream, and the areal proportion of each part within each plot averaged for all the study plots (n = 26). I regarded the mean areal proportion as the availability of each

part for bird foraging space. In addition, the frequency of prey attacks by birds observed in each part was determined by pooling the foraging data from all the study plots (number of prey attacks observed; 94 for flycatchers, 563 for gleaners, and 90 for bark probers). A preference value for each part by the birds was calculated separately for each foraging guild, using the formula of Jacobs (1974): $D = (r - p) / (r + p - 2rp)$, where D is the preference value for a part in the plots, r is the proportion of prey attacks observed in the part, and p is the areal proportion of the part in the plots (availability). The values range from –1 (never used) to +1 (only one range used), with negative and positive values indicating avoidance and preference, respectively, and 0 indicating that given part is used in proportion to its availability.

The contributions of aquatic and terrestrial prey to bird diets were estimated for each guild by using data obtained from the foraging observations. The frequency of each prey item was multiplied by the mean individual dry mass of that taxon, which was determined from the samples collected during study (T. Iwata, unpublished data). The percentage of dry mass contributed by each item was then determined separately for flycatchers, gleaners and bark probers. Further information on the treatment of foraging data was given in Iwata et al. (*in press* a).

Relationships between bird abundance and aquatic and terrestrial variables in the study plots (aquatic: stream length, stream width, local emergence and aquatic insect abundance; terrestrial: live tree density, snag density, mean dbh of live trees, mean dbh of snags and terrestrial aerial insect abundance) were analyzed for each foraging guild using simple linear regression analysis. When necessary, variables were ln (x) or ln (x+1) transformed to achieve homoscedasticity and linearity (Zar 1984). For guilds significantly related to at least one aquatic variable in the analyses, path analysis was further performed to detect more details pertaining to causality, because complicated causal schemes were likely to exist among the aquatic variables. Path analysis is a useful technique, since it can decompose the overall correlation between two variables into direct effects, indirect effects mediated by other variables, and spurious effects due to common causes (Mitchell 1993). Path coefficients indicate the amount of change in a dependent variable expected from a unit change in an independent variable, with any effect of other independent variables statistically held constant.

I considered that stream length and width affected bird abundance directly as structural characteristics of bird habitat. In addition, the indirect effects of both variables on birds via

aquatic insect abundance were likely to exist, because stream geomorphology alters the distribution and flux rate of aquatic insects (Power and Rainey 2000) and thereby may affect bird abundance. The lateral flux of aquatic insects also varies depending on the emergence rate (Power and Rainey 2000). Therefore, local emergence of aquatic insects was also considered as a potential factor affecting birds indirectly via a causal linkage with aquatic insect abundance. I constructed a path diagram connecting these variables to determine which causal relationship most contributed to bird abundance (see Fig. 3.4). Violations of the homoscedasticity and linearity of the relationships between the variables were countered by ln (x) or ln (x+1) transformation of data (Mitchell 1993). When the significant effect of exogenous variables (stream length, stream width, or local emergence) on birds was obtained in the path model, robust locally weighted regression (LOWESS: Cleveland 1979) was used to visualize the overall shape of its relationship by using the untransformed data.

RESULTS

Spatial distribution of aquatic and terrestrial aerial insects

The abundance of emerging aquatic insects decreased exponentially with distance from the stream (Fig. 3.2). In particular, the slope was very steep within 5 m of the stream, the abundance at that distance being only 19.6% of that above the stream surface. In contrast, the abundance of terrestrial aerial insects did not vary with distance from the stream (Fig. 3.2, see Iwata et al. *in press* a for detailed analyses).

Bird foraging space and prey items

Flycatchers and gleaners concentrated their prey attacks above streams or at stream edges, foraging considerably on adult aquatic insects. The preference value (D) indicated that flycatchers strongly selected space above the stream and within 5 m of the stream for foraging, whereas other parts ($\geq$ 5 m from stream) were rarely used (Fig. 3.3). Although sample size was small, the foraging observations showed that aquatic prey was the dominant prey item of flycatchers, accounting for 82% by dry mass of their diets (Table 3.2). Gleaners also exhibited a strong preference for the stream edge (0-5 m from stream) as a foraging space, avoiding the parts greater than 5 m distance from stream (Fig. 3.3). The contribution of aquatic prey to their diets

accounted for 67% in dry mass (Table 3.2). In contrast, bark probers did not exhibit a distinct preference for any part, although their strong avoidance of space above the stream was evident. Aquatic prey comprised only a small proportion (19%) of their diets.

Bird abundance in the riparian forest

Simple linear regression analyses revealed that the abundance of flycatchers and gleaners were both significantly related with stream length (flycatchers: $R^2 = 0.42$, $P < 0.001$; gleaners: $R^2 = 0.53$, $P < 0.001$) and aquatic insect abundance (flycatchers: $R^2 = 0.32$, $P = 0.003$; gleaners: $R^2 = 0.52$, $P < 0.001$, $n = 26$ for all). In contrast to these guilds, bark prober abundance was significantly related only with snag density (a terrestrial variable, $R^2 = 0.22$, $P = 0.016$, $n = 26$); the higher the snag density, the greater the abundance of bark probers. The other independent variables did not related to the abundances of all guilds ($R^2 = 0.001$-0.10, $P = 0.117$-0.909, $n = 26$ for all). Therefore, path analysis was performed for flycatchers and gleaners to evaluate which causal link associated with the aquatic variables most strongly explained their abundance.

The proposed path models significantly fitted the data obtained, and explained 49% and 72% of the variance in abundance of flycatchers and gleaners, respectively (Fig. 3.4). Non-significant goodness-of-fit tests indicated that no deviations occurred between observed and expected correlation matrices in the models (flycatchers: $\chi^2 = 0.80$, $P = 0.371$; gleaners: $\chi^2 = 0.03$, $P = 0.869$, df = 1 for each), indicating that both models are a valid explanation of the interactions. Flycatcher abundance was directly influenced by stream length, the path coefficient having a significant positive value (Fig. 3.4). Although stream length significantly affected aquatic insect abundance in the riparian forests, the direct effect of the latter on flycatchers was not significant. These results suggest that the significant positive relationship between aquatic insects and flycatcher abundance in the simple linear regression analysis was a spurious effect mediated by multiple positive effects of stream length on both variables (see Fig. 3.4). Consequently, the indirect effect of stream length on flycatchers via aquatic insect abundance was not significant. Similarly, gleaner abundance was directly influenced by stream length (Fig. 3.4). In addition, gleaner abundance was significantly affected by the indirect causal relationship with stream length via aquatic insect abundance. Stream width and local emergence did not significantly affect both guilds, path coefficients not differing significantly from zero in any causal links with those variables.

The robust locally weighted regression (LOWESS) described non-linear curves for the relationships between stream length and both flycatchers and gleaners (Fig. 3.5). Flycatchers steadily increased from 110 m to 150 m in stream length, but ceased to do so over greater lengths. Gleaner abundance doubled at about 170 m stream length compared with that at about 110-120 m length and levelled off over greater lengths.

DISCUSSION

Flycatchers and gleaners appeared to spatially track high concentrations of emerging aquatic insects. Most adult aquatic insects stayed close to the stream (particularly within 5 m of the stream), their abundance in the riparian forest declining exponentially with distance from the stream, as have been reported previously (e.g., Petersen et al. 1999, Delettre and Morvan 2000, Power and Rainey 2000). Regardless of terrestrial aerial insect distribution, being independent of the stream channel, flycatchers concentrated their foraging attacks on the spaces around the stream channel. Similarly, gleaners strongly selected the stream edge as a foraging space. Although gleaners showed no strong preference for the space above the stream channel, this was probably due to their foraging method in which they searched mainly for stationary prey along the stream banks rather than aerial prey (T. Iwata, *personal observation*, see Nakano and Murakami 2001). Both flycatchers and gleaners fed intensively on emerging aquatic insects. In addition to aquatic prey, gleaners also consumed arachnids to a substantial degree (23.5% of diet in dry mass). Although the Malaise-trap sampling did not quantify the abundance of spiders and harvestmen, those non-aerial predators were conspicuously abundant along the stream edges where they intensely consume emerging aquatic insects (C. Kato, S. Nakano and T. Iwata, unpublished data; see also Jackson and Fisher 1986, Henschel et al. 2001). Thus arachnids possibly mediate the energy transfer from streams to forest insectivorous birds. These results suggested that aquatic insect flux provided significant subsidies to flycatchers and gleaners in spring when terrestrial prey biomass was exceedingly low, and affected the spatial distribution of both bird guilds in the riparian forests. In contrast, bark probers, such as woodpeckers and nuthatch, preyed mainly upon wood-living insect larvae or pupae (mainly Coleoptera) by pecking or probing. Since the biomass of such prey organisms depends less on the seasonal change in forest production, bark probers do not necessarily rely on aquatic insects, with the result that they

avoided treeless stream channels.

The abundance of both flycatchers and gleaners were strongly affected by stream geomorphology, whereas that of bark probers was associated with snag density, a stand characteristic of the riparian forests. The positive relationship between the abundance of bark-probing species and snag density has been widely reported (Breininger and Smith 1992, Renken and Wiggers 1993), because snags provide preferred sites for their foraging or cavity nesting (Raphael and White 1984, Olsson et al. 1992). The path analysis indicated that the study plots with longer stream channels (i.e., higher channel sinuosity) had greater aquatic insect abundance. Increases in stream length within a plot can increase the amount of space close to the stream edge, as well as stream area, where emerging aquatic insects readily penetrate. Although stream width and local emergence also had positive (but not significant) effects on aquatic insect abundance, stream length had the more important effect. Thus, the increased density of stream edge, in addition to large area of stream surface, seemed to most strongly increase the flux of aquatic insects into the riparian forests. Such an increased flux of aquatic insects by stream meanders elevated gleaner abundance. In other riparian systems, birds of this type of foraging guild have also been shown as numerically responding to aquatic insect abundance (Davies 1976, Gray 1993, see also Gende and Willson 2001). In addition, their abundance was directly affected by stream length *per se*. This is probably because gleaners have increased in response to an increase in the stream edge (their preferred foraging space) accompanying longer stream channels or they have used structural characteristics of stream channels as a clue to identify high availability of aquatic prey, as shown by Orians and Wittenberger (1991). On the other hand, flycatcher abundance was only directly affected by stream length, with the indirect effect of stream length via aquatic insect abundance being not significant. Different from gleaners, the foraging method of flycatchers was restricted, the birds mainly capturing flying insects in the air (83.0% of prey attacks observed). Such a flycatching-technique (i.e., sally) may make it difficult for them to utilize stationary hiding arthropods, necessitating a remarkable dependence on aerial aquatic insects. Because stream meanders increase the space suitable for their foraging on aquatic insects (i.e., more open space adjacent to their perches; see Maurer and Whitmore 1981), it could be more responsible for determining flycatcher abundance than food availability. My results showed that although the causal links affecting bird abundance differed between flycatchers and gleaners, meandering stream channels apparently increased both insectivores in the riparian forests.

The LOWESS regression curve revealed that both flycatchers and gleaners increased with increasing stream length to some extent, but levelled off in plots greater than ~150 m and ~170 m length, respectively. Thus, the straightening of meandering stream channels may be expected to non-linearly influence both guilds. However, the curves had been fitted to untransformed data and expressed overall trends involving multiple causal interrelationships among aquatic- and unexplained-variables. Therefore, details of the mechanisms underlying these patterns need further investigations for clarification. For example, intra- and interspecific competition for limited space (e.g., territoriality) or limited food resource (e.g., aquatic insects) may act to prevent any increase in abundance in forests with longer stream channels (see Petit and Petit 1996, Rodenhouse et al. 1997).

In conclusion, the present study clearly showed that stream meanders exert powerful influences over adjacent riparian bird communities in a highly seasonal landscape. The high density of stream edge associated with meandering channels can support abundant insectivorous birds by facilitating the energy transfer from stream production. This suggests that the boundary shape, delimited by stream geomorphology, is a spatial feature that strongly affects the degree of trophic connectivity between forest and stream (Wiens et al. 1985, Stamps et al. 1987). To conserve the communities in a riparian landscape, it will be essential to maintain the interactive energy exchange between forest and stream. This cannot be accomplished without maintaining the functional integrity of the boundary form.

Table 3.1. Foraging guild and abundance of insectivorous bird species observed in the study plots.

Species	Mean number of birds per plot†
Flycatchers	
Narcissus flycatcher (*Ficedula narcissina*)	0.35 ± 0.49
Blue-and-white flycatcher (*Cyanoptila cyanomelana*)	0.29 ± 0.35
Brown flycatcher (*Muscicapa latirostris*)	0.20 ± 0.28
Gleaners	
Oriental cuckoo (*Cuculus saturatus*)	0.01 ± 0.03
Gray wagtail (*Motacilla cinerea*)	0.03 ± 0.13
Olive-backed pipit (*Anthus hodgsoni*)	0.09 ± 0.14
Brown-eared bulbul (*Hypsipetes amaurotis*)	0.36 ± 0.33
Bull-headed shrike (*Lanius bucephalus*)	0.01 ± 0.03
Winter wren (*Troglodytes troglodytes*)	0.06 ± 0.16
Japanese robin (*Erithacus akahige*)	0.02 ± 0.07
Siberian blue robin (*Erithacus cyane*)	0.01 ± 0.05
White's ground thrush (*Turdus dauma*)	0.01 ± 0.03
Gray thrush (*Turdus cardis*)	0.18 ± 0.18
Brown thrush (*Turdus chrysolaus*)	0.04 ± 0.10
Short-tailed bush warbler (*Cettia squameiceps*)	0.47 ± 0.51
Bush warbler (*Cettia diphone*)	0.24 ± 0.36
Pale-legged willow warbler (*Phylloscopus tenellipes*)	0.70 ± 0.54
Crowned willow warbler (*Phylloscopus occipitalis*)	0.71 ± 0.49
Long-tailed tit (*Aegithalos caudatus*)	0.22 ± 0.29
Marsh tit (*Parus palustris*)	0.36 ± 0.42
Coal tit (*Parus ater*)	0.24 ± 0.50
Varied tit (*Parus varius*)	0.12 ± 0.23
Great tit (*Parus major*)	0.74 ± 0.72
Japanese white-eye (*Zosterops japonica*)	0.02 ± 0.07
Black-faced bunting (*Emberiza spodocephala*)	2.70 ± 1.28
Eurasian jay (*Garrulus glandarius*)	0.15 ± 0.14
Bark probers	
Great spotted woodpecker (*Dendrocopos major*)	0.09 ± 0.14
White-backed woodpecker (*Dendrocopos leucotos*)	0.01 ± 0.03
Pygmy woodpecker (*Dendrocopos kizuki*)	0.22 ± 0.30
Nuthatch (*Sitta europaea*)	0.27 ± 0.34
Tree creeper (*Certhia familiaris*)	0.15 ± 0.28

†Means ± SDs determined by averaging abundance data from all study plots (0.5 ha, $n = 26$).

Table 3.2. Composition of prey items (% in dry mass) in the study plots for birds of each guild. Values were estimated from direct foraging observation data and mean individual dry mass of each prey item. The total number of prey (*n*) observed for each guild shown in parentheses.

	Aquatic prey					Terrestrial prey								
Guild	EPH	PLE	TRI	DIP	Total	HEM	COL	DIP	LEP-A	CAT	HYM	ARA	OTH	Total
Flycatchers (38)	12.3	26.0	20.0	24.0	82.3	0.0	6.7	1.7	0.0	0.4	0.7	8.2	0.0	17.7
Gleaners (272)	8.7	15.0	17.6	25.4	66.7	0.2	1.0	3.0	1.6	2.3	0.7	23.5	1.0	33.3
Bark probers (58)	0.0	2.5	1.9	14.8	19.2	0.0	34.8	0.0	8.5	0.8	5.3	28.4	3.0	80.8

Abbreviations: EPH, Ephemeroptera; PLE, Plecoptera; TRI, Trichoptera; DIP, Diptera; HEM, Hemiptera; COL, Coleoptera; LEP-A, Lepidoptera (adult); CAT, caterpillar; HYM, Hymenoptera; ARA, Arachnida; OTH, others.

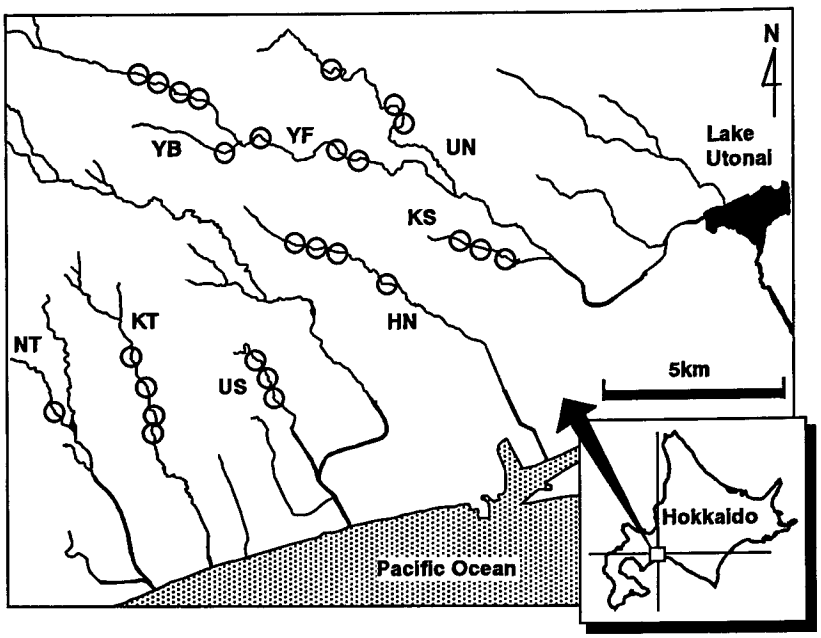


Fig. 3.1. Map of the study area with locations of the study plots (open circles) in Tomakomai City, southwestern Hokkaido, Japan. UN, Uenae Stream; YF, Yufutsu Stream; YB, Yuburi Stream; KS, Kumanosawa Stream; HN, Horonai Stream; US, Usunosawa Stream; KT, Koitoi Stream; NT, Nishitappu Stream.

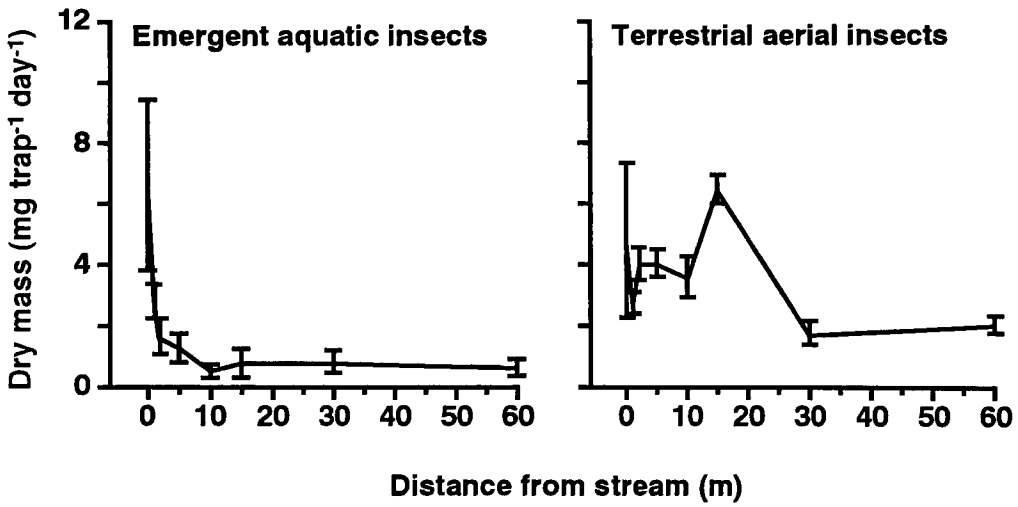


Fig. 3.2. Average abundance of aquatic and terrestrial aerial insects, collected at different distances from the stream channel by Malaise-trap sampling. Means ± SEs shown were determined by combining all data collected in two streams (Uenae and Horonai streams) during two sampling periods (10-16 May and 16-22 May) (n = 4 for each point).

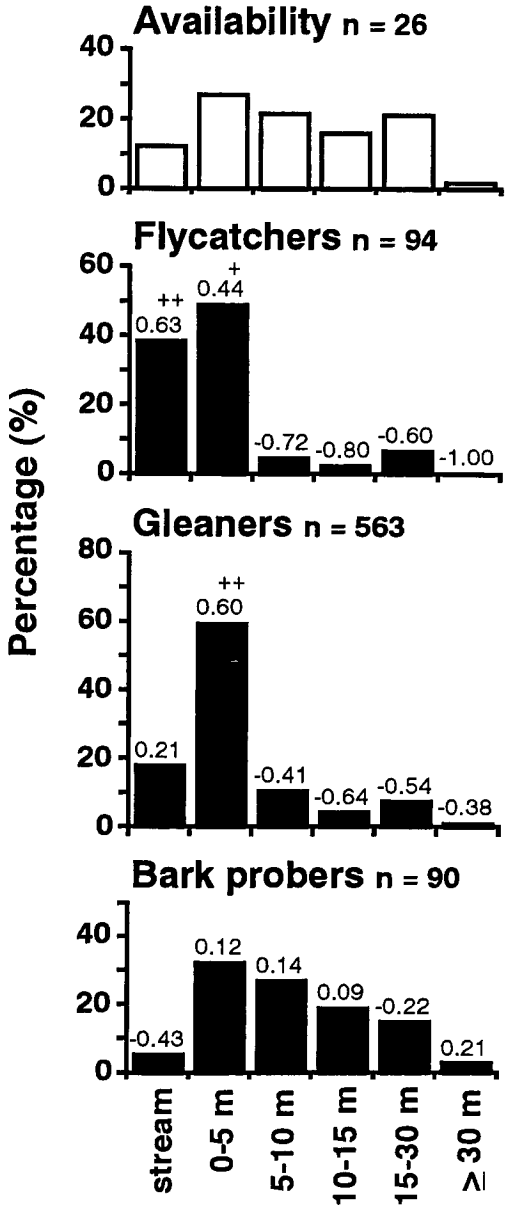


Fig. 3.3. Use of, and preference for, foraging space by birds of each guild in the study plots. Availability of each of six parts (0, 0-5, 5-10, 10-15, 15-30, and ≥ 30m from active stream channel) is the mean value of the areal proportion of the part in the study plots (n = 26). Jacobs selectivity index (D) is shown at each column. Positive selectivities are denoted by symbols for clarity: (+) values between 0.3 and 0.6; and (++) values > 0.6.

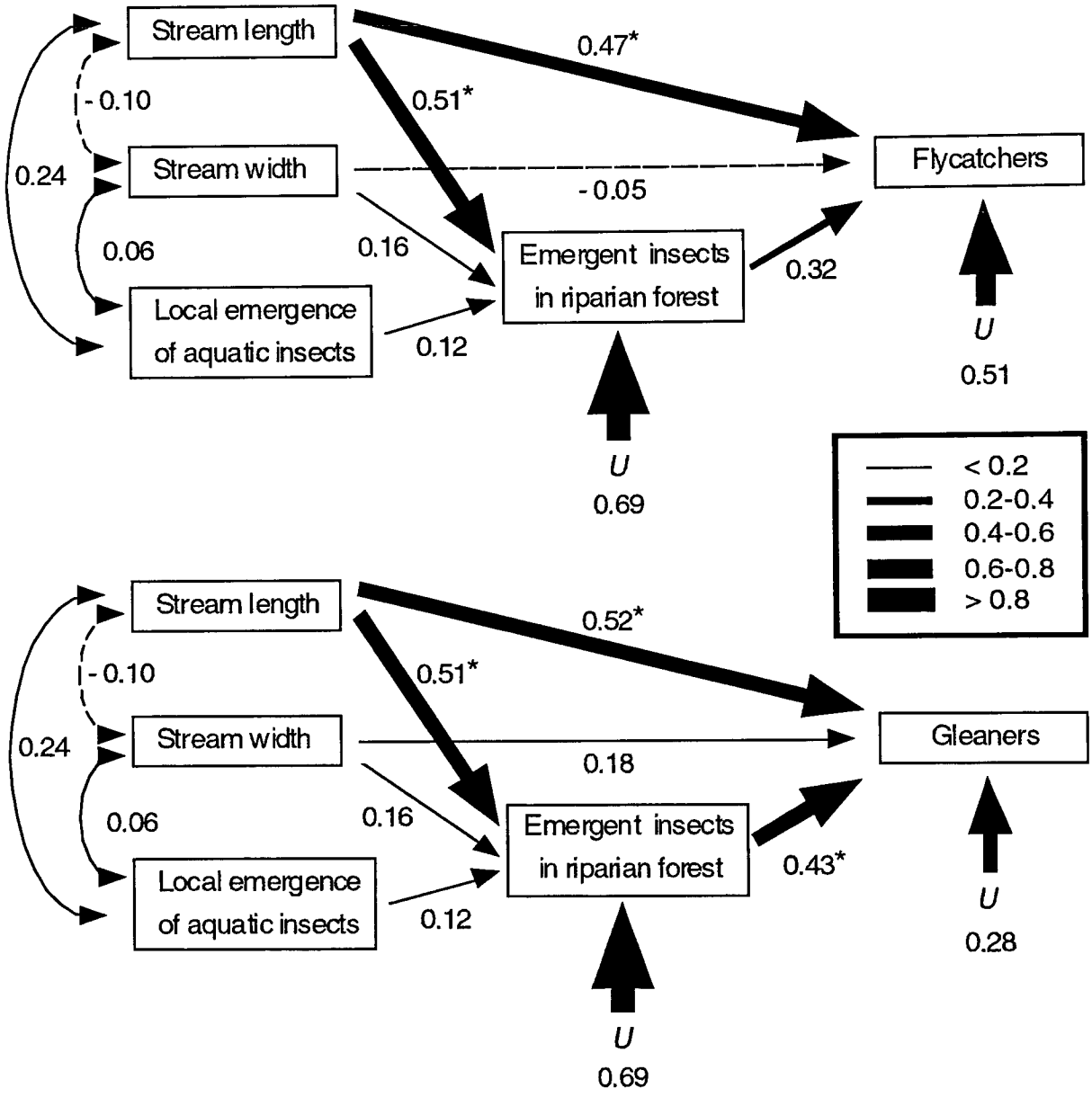


Fig. 3.4. Results of path analyses for flycatchers and gleaners. Dashed lines denote negative effects; solid lines positive effects. Arrow widths indicate value of path coefficients as presented in the enclosed box (actual values are shown by figures associated with arrows). Values associated with *U* indicate unexplained variance of dependent variables. Single asterisks indicate that path coefficients are significantly different from zero ($P < 0.05$). Flycatcher abundance, gleaner abundance, stream length and stream width were ln (x) or ln (x+1) transformed in the analyses.

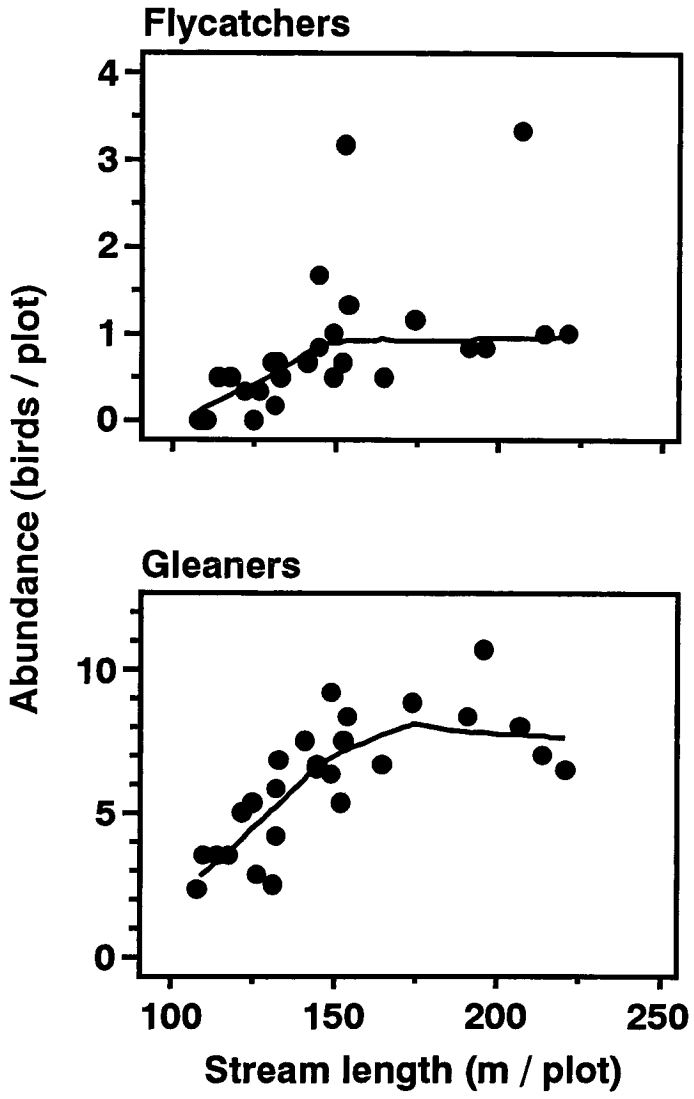


Fig. 3.5. Relationships between stream length and both flycatchers and gleaners in the study plots. Each data point is for one study plot. Solid lines in data field are LOWESS regression curves.

CHAPTER 4
DRAINAGE NETWORKS DICTATE BIRD ASSEMBLAGE STRUCTURES IN TEMPERATE FORESTED BASINS

In the previous chapter, I showed that riparian forests with more highly sinuous streams can sustain more birds, because meandering reaches elevate aquatic prey abundance in the forest by increasing the amount of both stream edges and stream surface where adult aquatic insects concentrate (Chapter 3). This result allows me to extrapolate such fluvial geomorphic impacts on bird populations to drainage basin scale. Drainage basin is a landscape unit delineated by watershed divides that form a spatially discrete hydrological system. Within the system, stream networks not only route the material flow downstream but function as energy artery to transport stream products to the neighboring terrestrial communities (e.g., via aquatic insect emergence). Because the lateral flux of adult aquatic insects dose not penetrate into forests distant from streams (Petersen et al. 1999, Power and Rainey 2000, Iwata et al., *in press* a), many insectivorous birds are expected to strongly depend upon stream channels as their prime habitats, especially during the periods when terrestrial resource is depleted (Gray 1993, Iwata et al., *in press* a). If this is the case, the development of drainage network structures may influence the bird populations at the basin level of resolution. In this chapter, I conducted a field survey in temperate forested basins to verify the hypothesis that well-developed drainage networks sustain more birds during spring when terrestrial prey abundance is low. The analyses involved the distribution of invertebrate prey, and foraging behavior, abundance, and species richness of bird assemblages in a number of census plots established within drainage basins in spring (May–June) and summer (July-August) periods.

METHODS

Study area

The study was conducted from May to August 2001 in eight drainage basins that differ in the development of drainage network structure (Fig. 4.1 and Table 4.1). Those drainage basins

discharge into the Pacific Ocean through Shiraoi Town (42°34'N, 141°21'E) or through Tomakomai City (42°38'N, 141°36'E) in southwestern Hokkaido, Japan. The upper parts of the drainage basins were located within the National Forest, which did not encompass residential areas. I selected those non-populated areas as study area that covers a total of 19,070 hectares (Fig. 4.1 and Table 4.1). The study area lies in the cool-temperate region with a mean annual temperature of about 7 °C. The mean annual precipitation is ~1,600 mm; snowfall is about one-fourth of annual precipitation. The study area have been the region of intense volcanic activity; a large amount of pyroclastic-flow deposits covers the study area (Fujiwara 1987, Yamazaki 1991). Permeable volcanic rocks may form less developed drainage network since most of the water percolates downwards so that little surface erosion or channel formation may take place (Suzuki et al. 1985, Oguchi 1997). Therefore, the notable difference in the drainage network development among the basins may have been the results of the spatially heterogeneous distribution of pyroclastic-flow deposits and the difference in time elapsed following the previous eruptions.

With 1:50,000 scale vegetation and forest management maps, the landscape elements within the drainage basins were classified as either broad-leaved deciduous forest, coniferous forest, alpine forest, dwarf bamboo grassland (*Sasa* spp.), recent clearcuts (< 5 years old), pasture, or natural outcrop (Fig. 4.1 and Table 4.2). Streams could be identified only as lines on the maps because their wetted widths are usually less than 10 m. Of those landscape elements, the dominant habitat types were deciduous forest and coniferous forest, which together accounted for > 85% of the study area (range = 87.7-98.8%, Table 4.2). The overstory of the deciduous forests is dominated by Japanese white birch (*Betula platyphylla* var. *japonica*), alder (*Alnus hirsuta*), oak (*Quercus crispula*), Japanese cucumber tree (*Magnolia obovata*), ash (*Fraxinus mandshurica*), painted maple (*Acer mono*) and Japanese maple (*Acer palmatum* var. *matsumurae*). Coniferous forests mainly consist of Sakhalin fir (*Abies sachalinensis*), Yezo spruce (*Picea jezoensis*), Sakhalin spruce (*Picea glehnii*) and Japanese larch (*Larix leptolepis*), most of which were planted after clearcutting of natural forests by national forestry practices during the past several decades. In the study area, most deciduous tree species broke bud from mid to late May, developed leaves throughout June, and leafed out in early to mid July. In this study, spring and summer periods were defined as April-June and July-August, respectively. The field survey was initiated after confirmation of the arrival of most summer breeding migrants (from late April to early May) and completed before those birds began to depart the study area

(from mid to late August).

A total of 269 circular plots (50 m radius, 0.8 hectare area) were established over the eight drainage basins to census bird populations (Fig. 4.1). Although the effect of drainage networks on bird assemblages was of the greatest interest in this study, effects of various landscape elements were also investigated to gain a knowledge of the overall bird population in each drainage basin. Bird census plots were therefore placed so as to cover various types of local habitat and landscape structures. Individual census plots were separated by at least 200 m. A hand held GPS unit (Model 38, Garmin International Incorporated, Olathe, Kansas) was employed to obtain latitude and longitude coordinates of each census plot.

Invertebrate sampling and analyses

Distributional patterns of potential flying prey for birds (both adult aquatic insects and terrestrial aerial insects) were surveyed as a function of stream proximity by Malaise-trap sampling (Townes 1972). A line transect, running at a right angle to the stream channel, was established for each of a small stream (≤ 10 m wetted width) running through a deciduous forest (Tarumai Basin), a small stream in a coniferous forest (Oboppu Basin), a large stream (> 10 m wetted width) in a deciduous forest (Shikiu Basin), and a large stream in a coniferous forest (Syadai Basin; four transects in total). Elevation range (130-350 m) were similar among transects. Half-sized Malaise traps (see Chapter 3) were deployed concurrently along each transect at distances of 0 (over stream), 1, 10, 100, and 1,000 m from the stream channel (80 cm above the stream surface or ground). All traps set above stream surface were located within riffle habitats to exclude effects of stream channel-unit types on the emergence rate of aquatic insects (see Chapter 2). The traps were operated five sessions (four-six day intervals) during each of spring (2 May-1 June) and summer (12 July–16 August) periods (n = 5 per sampling point per season). The abundances of adult aquatic insects and terrestrial aerial insects at each sampling point were determined in the same manner as described in Chapter 3 and expressed as dry mass per trap per day (mg $trap^{-1}$ day^{-1}).

The biomass of foliage invertebrates was also surveyed at the sampling points. Invertebrates on the foliages at ~2-m high were collected quantitatively from three branches chosen randomly around each sampling point. A branch was held onto a tray (1 m x 1 m area) and beaten repeatedly, and all invertebrates dropped onto the tray were collected. In addition,

leaves were carefully checked, and remaining invertebrates were collected. This sampling procedure was made three times at two-wk intervals during each of spring (6 May-5 June) and summer (7 July-10 August), producing a total of nine samples (three branches x three times) per sampling point in each season. The samples were examined in the same manner as for the Malaise-trap samples. The biomass of foliage invertebrates was then expressed as dry mass per unit area (mg/m^2).

Bird observations

The fixed-radius point count method was used to estimate bird abundance and species composition at each census plot (Hutto et al. 1986). All plots were visited once during each of spring (2 May-8 June) and summer (4 July-9 August) periods. Bird counts were conducted from dawn until about 1100 h on days not affected by rain, fog or strong wind. Upon arrival at a census plot, the observer waited for 5 min and then recorded all birds seen or heard within the maximum radius of 50 m during a 15-min observation period. Birds that flew over a plot without landing were not included in the data for that plot. The observer attempted to record each individual only once during each observation.

After the completion of bird counts in each census plot, bird foraging behavior was observed up to a total of 15-min period. The observation was made according to the method described in Chapter 3 (see also Iwata et al. *in press* a). To ensure sufficient sample sizes, additional observations for bird's foraging behavior were implemented during 9-13 June and during 10-16 August in a wide variety of habitat types within the eight drainage basins. In addition, the observer always attempted to record any foraging behaviors and prey items, whenever he confirmed during the study.

A total of 58 bird species was observed during the study, comprising 25 species of year-round residents and 33 species of summer breeding migrants (Table 4.3). All birds observed were classified into the following six foraging guilds, flycatchers, gleaners, bark probers, stream foragers, raptors or herbivores (Table 4.3). Flycatchers, gleaners and bark probers were classified in the same manner as described in Chapter 3. The other foraging guilds were classified as follows: dipper and kingfisher, both of which feed under running water, were stream foragers; finches, buntings, pigeons, pheasant, grouse, and nutcracker were herbivores because they usually feed on plant materials including seeds, buds and berries; hawks and owls were grouped

into raptors. For each census plot, the bird abundance of each foraging guild was determined separately for spring and summer periods. In addition, bird species richness was calculated for each season as the total number of species recorded in each census plot during the 15-min count.

Environmental measurements for census plots

By reference to Estades and Temple (1999) and Drapeau et al. (2000), I measured or calculated sets of environmental variables differing in spatial coverage (local habitat, landscape position and landscape composition variables; Table 4.4), with the aid of a geographic information system (GIS; ArcView 3.1, ESRI Japan, Inc., Tokyo). Local habitat variables reflect structural attributes of microhabitat in each census plot. Landscape position variables reflect the location of each census plot and its spatial arrangement relative to the various landscape elements. Landscape composition variables are the composition of landscape elements surrounding each census plot. For the environmental measurements, I obtained GIS layers of digital elevation model (DEM) with 30 m grid size, 1:25,000 scale digitized topographical maps, and 1:50,000 scale digitized vegetation maps.

In every census plot, local habitat variables, including vegetation structure and slope, were quantified. During each of spring and summer periods, the measurement of vegetation structure was made once in each census plot on the day when the bird count was conducted (Table 4.4). Five quadrats (10 m x 10 m area) were established in each census plot as follows: one at the center of the plot and the others oriented in the cardinal compass directions 30 m from the center. In each quadrat, I estimated percent cover of vegetation in five layers (0-0.5 m, 0.5-2.5 m, 2.5-5 m, 5-10 m, >10 m) using a semiquantitative scale (0, 1-25, 26-50, 51-75, >75%). The percent vegetation cover was coded as follows: 0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75% and 4 = > 75%. The coded values of the five quadrats was averaged for each layer and used to express vegetation cover within each census plot. In addition, the number of standing dead trees (snags) > 5 cm in dbh was recorded in each quadrat and averaged for each census plot. Slope within a circular area (100 m radius) surrounding each census plot was calculated using DEM.

Landscape position was quantified for each census plot using six variables derived from DEM, and the topographical and vegetation maps (Table 4.4). Elevation, the nearest distance to stream, and the nearest distance to each of habitat types (deciduous forest, coniferous forest, alpine forest, and nonforest area) were calculated. In this measurement, dwarf bamboo grassland,

recent clearcuts, pasture, and natural outcrop were grouped into nonforest area. When a census plot was located within a focal habitat type, the distance to the habitat from the census plot was given to 0 m.

Landscape composition surrounding each census plot was measured in concentric circles increments of 250, 500, 1,000 m radii. The proportion of area occupied by each forest and nonforest habitat types within each circle was calculated using the vegetation maps (Table 4.4). Consequently, a total of 26 environmental variables was quantified for each census plot.

Environmental measurements for drainage basins

Drainage basin properties, including geomorphic characteristics and landscape composition of each drainage basin, were measured in order to identify landscape variables that may influence bird abundance at the basin level of resolution (Tables 4.1 and 4.2). Means of elevation (m) and slope (degree) within each drainage basin were calculated from the 30 m elevation grid cells (DEM) contained within the basin. Relative relief (R) is a dimensionless parameter of the relief characteristics of a drainage basin, and expressed as $R = H/A^{0.5}$, where H is the elevation difference between the highest and lowest points in the basin and A is the basin area. Drainage network was quantified by drainage density, drainage frequency and bifurcation ratio, all of which are useful measures of the frequency and spacing of streams within the drainage basin (Horton 1945, Strahler 1952). Drainage density (km/km^2) is the ratio of total stream length within a drainage basin to the total basin area, which was calculated with the digitized topographical maps. Drainage frequency (streams/km^2) is the number of first-order streams per unit area of drainage basin. Bifurcation ratio is the ratio between the number of streams of one order and those of the next higher order. Thus, the ratio is dimensionless denoting the branching pattern of streams in a drainage network. For each drainage basin, bifurcation ratios of every stream order were averaged for whole basin and used in analyses. Percentage composition of landscape elements, including deciduous forest, coniferous forest, alpine forest and nonforest area, was calculated for each drainage basin using the vegetation maps. Consequently, a total of ten environmental variables were quantified for each drainage basin.

Data analyses

The effects of the distance from stream and season on the abundances of potential flying prey

(adult aquatic insects and terrestrial aerial insects) were analyzed separately for the four line transects, using two-way analysis of variance (ANOVA). Two-way ANOVA was also performed on the biomass of foliage invertebrates, with the distance from stream and season as main factors. In the latter analysis, however, adult aquatic insect biomass was not analyzed since those insects were rarely collected from foliages (mean biomass, spring, 0.22 ± 0.09 SE mg/m^2; summer, 0.60 ± 0.12 SE mg/m^2, n = 180 for both periods).

To identify environmental variables that are important in determining the distribution of bird species, canonical correspondence analysis (CCA) was performed with the CANOCO program (ter Braak and Smilauer 1998). The CCA is a nonlinear eigenvector ordination technique especially designed for direct analysis of the relationships between multivariate ecological data sets (ter Braak and Smilauer 1998). In this analysis, data on species presence/absence and 26 environmental variables for bird census plots were analyzed separately for spring and summer periods. Environmental variables entering the final model were selected at the 5% significance level by a stepwise forward selection procedure (ter Braak and Smilauer 1998). The species scores obtained were used in the ordination plot.

Stepwise multiple regression analysis was performed separately for spring and summer periods, in order to identify the best predictors of environmental variables that explain bird abundance. In the analysis, the abundances of flycatchers, gleaners, bark probers, herbivores and all birds were included as dependent variables, but stream foragers and raptors were excluded because of their low abundances (stream foragers, 0.06 ± 0.02 SE birds/plot [spring], 0.04 ± 0.01 SE birds/plot [summer]; raptors, 0.004 ± 0.004 SE birds/plot [spring], 0.02 ± 0.01 SE birds/plot [summer], n = 269 for all). Environmental variables contributed significantly to the CCA models were included in the regression analyses as independent variables. An independent variable was allowed to enter the model when $P \leq 0.05$. I confirmed that the best predictors obtained from this procedure did not differ from those derived from multiple regression models that included all of the 26 environmental variables as independent variables. Robust locally weighted regression (LOWESS: Cleveland 1979) was used to visualize the overall shape of the relationship between the abundance of each foraging guild and the environmental variable selected as the best predictor. The LOWESS regression line was also fit to species richness of each census plot against the selected environmental variable.

Finally, Pearson product-moment correlation coefficients were calculated between each

of ten drainage basin properties (Table 4.7) and mean bird abundance within a drainage basin. Each drainage basin was first divided into several habitat components, according to landscape variables that strongly influenced bird abundance. Second, the average bird abundance was calculated for each habitat component using the data of census plots contained within the component. Third, I multiplied the average abundance by the percentage of the area that habitat component covers the drainage basin. Finally, those values obtained from every habitat component were summed for each drainage basin so as to estimate the area-based, habitat-weighted average of bird abundance in each drainage basin (birds/plot). Mean species richness (species/plot) was also calculated for each drainage basin in the same way as above and examined to clarify its relation to the drainage properties that were significantly correlated with the mean bird abundance. Uncertainties of those estimates (i.e., standard errors) were determined by considering the propagation of errors in the above calculations (Taylor 1982).

In all analyses, except CCA, coal tit (*Parus ater*) was excluded from the abundance data of gleaners, since this species was occasionally observed to move about in large flocks (11-37 birds) after fledgling period, which resulted in that gleaner abundance at several census plots where the observer haphazardly encountered such flocks deviated greatly from those at the other plots. All variables, except species presence/absence data and variables used for LOWESS, were $\log_{10}(x + 1)$ or $\log_{10}(x)$ transformed for exact values or arcsin ($p^{0.5}$) transformed for percentage values to standardize variances and improve normality.

RESULTS

Distributions of aquatic and terrestrial prey

Adult aquatic insects were highly clumped around stream channels and their abundance decreased with distance from streams (Fig. 4.2). Two-way ANOVA on the aquatic insect abundance showed the significant effects of the distance from stream for all of the four line transects (Table 4.5). Although there were significant interaction effects (distance by season) in most of the transects, no significant effects of season were detected for three of the four transects, indicating that the flux of emerging aquatic insects from streams was similar between spring and summer periods. In contrast, terrestrial aerial insects were not affected by stream proximity, with two-way ANOVA showing no significant effects of the distance from stream for three of the four

transects (Table 4.5). However, significant effects of season were detected for all transects; abundance of terrestrial aerial insects was lower levels in spring than in summer (Fig. 4.2).

The spatial distribution of terrestrial foliage invertebrates was similar to that of terrestrial aerial insects (Fig. 4.3). According to two-way ANOVA, neither the effects of the distance from stream nor interaction effects (distance by season) on their biomass were significant for most of the transects (Table 4.5). These indicate that the distribution of terrestrial invertebrates on foliages was not strongly affected by stream proximity. However, effects of season were significant for all transects; biomass of terrestrial foliage invertebrates was very limited during spring and dramatically increased in summer (Fig. 4.3). Caterpillars, including the larvae of moth (Lepidoptera) and sawfly (Symphyta), contributed to a great proportion of the total biomass of foliage invertebrates in any place during summer period.

Bird prey items

A total of 956 and 951 prey items could be identified or inferred from the direct observations on bird foraging behaviors in spring and summer, respectively. The diet composition of each foraging guild was estimated from the frequency of prey items eaten by birds and is shown by different distances from streams in Fig. 4.4. Although sample sizes were small, the foraging observations showed that aquatic prey (mainly midges, craneflies, and caddisflies) was the dominant prey item of flycatchers (89% of their prey attacks) and gleaners (71%) around stream channels (< 50 m from stream channels) during spring period. Herbivores and, to a lesser extent, bark probers also preyed upon adult aquatic insects (mainly midges and craneflies) around streams, aquatic prey accounting for 48% and 26% of their prey items, respectively. Similar to the spatial distribution of adult aquatic insects, the contribution of aquatic prey to bird diets decreased with distance from streams. In summer period, the contribution of aquatic prey became less important (Fig. 4.4), despite the fact that the flux of aquatic insects from streams to forests remained constant from spring to summer (Fig. 4.2). In summer, aquatic prey comprised only a small proportion (< 30%) of the diets for all foraging guilds even around stream channels, instead caterpillars or the other terrestrial invertebrates increasing their contributions to bird diets.

Bird distribution and environmental variables

The ordination diagrams of the canonical correspondence analyses showed significant

associations between species distributions and environmental variables (Fig. 4.5). In the spring CCA plot, the distance to the nearest deciduous forest (DNDF), the distance to the nearest stream (DNS), and elevation of census plots (elevation) increased along the first ordination axis, whereas the vegetation covers of herbaceous layer (HER) and 0.5-2.5 m layer (UC2) and elevation decreased along the second axis. The majority of insectivorous species, including flycatchers, gleaners, stream foragers and bark probers, fell within the left side of the CCA plot center (Fig. 4.5). Of 37 species belonging to those foraging guilds, species positioned on the right side of the midpoint were only seven species: goldcrest, coal tit, Oriental cuckoo, jungle crow, Eurasian jay, great spotted woodpecker and Siberian blue robin (Table 4.3). These results indicated that most insectivorous birds had their center of distribution in census plots with DNDF, DNS and elevation below averages (DNDF ≤ 65 m, DNS ≤ 356 m, elevation ≤ 266 m). The CCA axis-2 strongly influenced the presence/absence of some bird species, such as jungle crow, gray wagtail, white wagtail, Siberian bluechat and black kite; census plots located in lower elevation with sparse vegetation covers of herbaceous and understory layers tended to have higher occurrence of those birds (Fig. 4.5 and Table 4.3).

Similar to the CCA plot for spring, DNDF, DNS and elevation increased along the first ordination axis in the summer CCA plot, and elevation and HER decreased along the second axis (Fig. 4.5). Associations between bird distributions and environmental variables in summer were less clear when the guild approach was taken, but seasonal shifts in the distributional patterns from spring were detected. Although stream foragers stayed near streams close to deciduous forests, the other insectivorous birds, especially birds belonging to gleaners, shifted their distributions to habitats more distant from streams and distant from deciduous forests with higher elevations than habitats used in spring (Fig. 4.5 and Table 4.3). Herbivorous species also showed pronounced seasonal shifts, in which they had higher occurrence probability in plots with higher elevation, compared with spring period.

The abundances of most foraging guilds were associated with landscape position and local habitat variables in both spring and summer periods, with stream proximity being the best predictor in most cases (Table 4.6). Stepwise multiple regression indicated that the spring abundances of flycatchers, gleaners, herbivores and all birds were best explained by a combination of DNS and DNDF, with the negative effect of the former being greater. Only bark prober abundance was not predicted by DNS in spring; they were more abundant in census plots

closer to deciduous forests in lower elevation. The LOWESS regression curves were fit separately for the abundance data of deciduous and coniferous forests, which showed that gleaners exponentially decreased with distance from streams in both forest types during spring period (Fig. 4.6). Flycatchers and herbivores also attained greater abundance around stream channels, although the effect of stream proximity on herbivores was weak relative to gleaners. Because gleaners overwhelmingly predominated in the bird assemblages, the total abundance of birds also decreased exponentially with distance from streams. In particular, the slope was very steep within 50 m from the streams. For all guilds, deciduous forests tended to have greater bird abundance than coniferous forests (Fig. 4.6).

The dependence of birds on stream channels changed seasonally. Although stepwise multiple regressions for the summer abundance showed that flycatchers and gleaners were also best modeled by a combination of DNS and DNDF and all birds were by DNS and HER (Table 4.6), the LOWESS regression lines for their abundances against DNS had apparently gentler slopes than those in spring (Fig. 4.6). These results imply that in summer, birds moved away from stream channels where they aggregated in spring period.

Similar to the spatial distribution of birds, species richness also decreased exponentially with distance from streams in both deciduous and coniferous forests in spring (Fig. 4.7). In summer, however, the effect of stream proximity on species richness became weaker than that in spring. This seasonal change was in good agreement with the seasonal shift in bird abundance. The shapes of LOWESS regression lines for species richness were nearly identical to those drawn through the scatterplot between DNS and total bird abundance in the corresponding period (Figs 4.6 and 4.7). In fact, total bird abundance in census plots was strongly correlated with species richness in both spring ($r = 0.94$, $P < 0.0001$) and summer ($r = 0.88$, $P < 0.0001$, $n = 269$ for both).

Bird abundance, richness and drainage basin properties

I divided each drainage basin into several habitat components, according to both vegetation types (deciduous forest, coniferous forest, and nonforest area) and the distance from streams (0-50, 50-250, and > 250 m), because those variables best explained the variations in bird abundance in this study area. Mean values of abundance and richness in each component was then used to estimate the habitat-weighted mean abundance and richness at basin scale. Pearson product-moment

correlation showed that mean spring bird abundance was only positively correlated with drainage density; drainage basins with longer stream channels per unit area had greater abundance of birds (Table 4.7 and Fig. 4.8). Even in summer period, when birds tended to disperse from stream channels, the mean abundance within a drainage basin was only positively correlated with drainage density (marginally significant, $P = 0.050$). Mean species richness was also positively correlated with drainage density in both spring ($r = 0.74$, $P = 0.035$) and summer ($r = 0.72$, $P = 0.044$, $n = 8$ for both) (Fig. 4.8).

DISCUSSION

The present chapter showed that landscape position variables and some local habitat features, related to understory vegetation structure, strongly influenced bird distribution in the drainage basins. In spring, many insectivorous bird species exhibited the higher occurrence probability in habitats located in relatively closer proximity to streams and to deciduous forests in lower elevation (Fig. 4.5). Of variables significantly associated with species occurrence, stream proximity was the most important in contributing to the spatial variation in bird abundance (Table 4.6). In fact, the abundances of flycatchers, gleaners and all birds decreased drastically with distance from stream channels, especially in spring (Fig. 4.6). These findings support a general argument that riparian forests sustain more abundant avifauna than do the surrounding uplands (Knopf and Samson 1994, Lachavanne and Juge 1997, Wiebe and Martin 1998). However, the effects of those environmental features on bird distribution got weak in summer, because their prime habitats were shifted to places distant from streams and distant from deciduous forests with high elevations, relative to spring habitats (Figs 4.5 and 4.6). The results imply that the degree to which riparian habitats support bird populations changes according to the season (see Rice et al. 1980, Wiebe and Martin 1998).

The preference for riparian habitats by birds is often resulted from the use of riparian buffer strips as movement corridors during the migration (Rice et al. 1980, Machtans et al. 1996) and from the diverse and structurally complex riparian vegetation, which can provide abundant nesting habitats (Stauffer and Best 1980, Knopf and Samson 1994, Wiebe and Martin 1998). However, since this study was initiated after most species had established territories, the 'corridor effect' cannot explain the strong associations of spring birds with stream channels. In

addition, because no strong association between spring bird distribution and vegetation covers was found (Fig. 4.5), except understory cover that negatively influenced some bird species (e.g., jungle crow, wagtails, Siberian bluechat and black kite), the dependence of birds on riparian habitats cannot be attributed to the streamside vegetation structures. Keast (1990) pointed out that food limitation often become a factor that most strongly influences the structure of bird assemblages in highly seasonal environments (see also Holmes 1990). In particular, considerable attention has recently been paid to the role of emerging aquatic insects in supporting bird assemblages under conditions of terrestrial food scarcity (Keast 1990, Nakano and Murakami 2001, Power 2001, Iwata et al., *in press* a). My foraging observations, in fact, showed that forest birds, especially flycatchers and gleaners, depended highly on emerging aquatic insects around stream channels in spring when terrestrial prey biomass was exceedingly low (Fig. 4.4). Even herbivores preyed upon aquatic prey around streams in spring. Furthermore, the aggregation of those birds around streams in spring appeared to spatially track the distributional pattern of aquatic prey (i.e., most adult aquatic insects stayed close to the stream) rather than terrestrial prey (Figs 4.2 and 4.6, see also Power and Rainey 2000, Iwata et al., *in press* a, Chapter 3). Thus, I conclude that trophic transfer of stream productions to terrestrial environments via aquatic insect emergence played a crucial role in determining the spatial distribution of spring birds.

In summer, however, major foods of forest birds were mainly comprised of terrestrial prey, such as caterpillars, arachnids and other terrestrial invertebrates (Fig. 4.4). In other temperate forests as well, caterpillars are the most important prey item fed to young birds during breeding period (Holmes 1990, Keast 1990, Nakano and Murakami 2001). In this study area, those terrestrial invertebrate abundances dramatically increased from spring to summer regardless of habitats (Figs 4.2 and 4.3). Therefore, despite the fact that aquatic prey flux in summer was of similar magnitude with that in spring, many insectivorous birds would cease to aggregate around streams as terrestrial prey became plentiful across the drainage basin. These findings suggest that bird distribution within the drainage basins is influenced by landscape attributes, in conjunction with prey availability that varies strongly over space and time. In particular, streams and adjacent forests offer the most important habitats for forest birds by supplying emerging aquatic insects in the period when terrestrial resource is restricted.

In addition to abundant bird populations, forests adjoining streams supported relatively rich avifauna (Fig. 4.7). Interestingly, the abundance and species richness in census plots were

highly correlated with each other in both spring and summer ($r \geq 0.88$), which resulted in that both assemblage properties traced similar trajectories against the distance from the nearest stream in the corresponding period. There are at least three mechanisms that would cause these patterns. First, riparian areas with higher habitat complexity may sustain more diverse and abundant birds (MacArthur et al. 1962, Roth 1976), which can generate the abundance-richness association. However, this mechanism does not provide a full explanation for their strong association seen throughout the drainage basin. Second, habitats supporting more individual birds may simply increase the likelihood of encountering many species than habitats with lower bird density, which is obvious but may not be a sufficient explanation. Third, the influence of inter- and intraspecific competition might partly explain this association. In the breeding season, I often observed chasing or countersinging by males in conspecific encounters, whereas heterospecific individuals were usually ignored (T. Iwata, *personal observation*). These indicate that the intensity of interspecific interference competition was low in this temperate breeding ground (see Hill and Lein 1989, Bourski and Forstmeier 2000, Forstmeier et al. 2001). Therefore, suitable habitats (e.g., riparian areas) can allow heterospecific individuals to increase more easily than conspecific ones, which is likely to increase species richness as a simple function of abundance. However, this argument is inapplicable in the summer case, because birds tended to weaken the competitive interactions in summer as the fledglings leave the nests and breeding communities are disbanded (T. Iwata, *personal observation*). Thus, further studies were needed for more proper understanding of the abundance-diversity relationships.

The present study showed that abundance and diversity of bird assemblages were the highest at the junction of forests and streams in the drainage basins. Moreover, I found that these influences of streams on birds extended over the whole basin scale. In fact, drainage basins with longer stream channels per unit area had greater abundance of birds (Fig. 4.8). This may be, at least in part, due to the fact that stream networks affected the magnitude of energy transfer from stream to forest ecosystems. In addition, such effect continued from spring through summer periods. This suggested that birds did not move much in summer from the spring habitats, even though their dependence on streams was relatively weakened. Furthermore, species diversity was also higher in basins with higher drainage density in both spring and summer (Fig. 4.8). These results indicated that despite the relatively small areas, stream habitats play disproportionately large roles in influencing the breeding density and diversity of bird assemblages at drainage basin

scale. Although strong effects of drainage density were detected during the study period, I did not do the investigation in autumn and winter seasons. However, Nakano and Murakami (2001) documented that year-round resident birds depend, again, upon emerging aquatic insects from autumn through winter, when terrestrial prey becomes depleted (or absence) while aquatic insects continue to emerge from streams. Therefore, drainage network structure in this temperate forested region may possibly be a crucial landscape feature in maintaining not only summer migrants but also resident bird populations throughout the year.

Table 4.1. Numbers of census plots and hydro-geomorphic parameters of eight study drainage basins.

Drainage basin	No. plots	Basin area (km^2)	Discharge (m^3/sec)†	Mean elevation (m)‡	Basin slope (degree)	Relative relief (dimensionless)	Drainage density (km/km^2)	Drainage frequency (streams/km^2)	Bifurcation ratio (dimensionless)
Oboppu	38	25.5	0.53	293 (1,000-35)	6.3	0.19	0.60	0.27	2.8
Tarumai	31	22.9	0.98	323 (995-72)	10.9	0.19	0.92	0.35	3.0
Betsubetsu	27	13.9	0.80	354 (835-44)	11.0	0.21	1.34	0.29	4.0
Syadai	34	29.9	1.46	361 (661-55)	8.7	0.11	0.54	0.20	2.5
Uyoro	42	20.9	1.92	381 (910-120)	12.3	0.17	1.74	0.72	2.5
Shikiu	43	50.9	5.76	577 (1071-89)	15.0	0.14	1.05	0.47	3.0
Tobyu	31	18.6	1.46	381 (897-67)	14.0	0.19	0.52	0.32	2.5
Meppu	23	8.1	0.39	206 (531-50)	14.0	0.17	1.08	0.50	2.0

† Discharge measured at the lowermost end of the study basin in a base-flow condition during the study.

‡ Range shown in parenthesis.

Table 4.2. Landscape compositions of eight study drainage basins.

Drainage basin	Deciduous forest (%)	Coniferous forest (%)	Alpine forest (%)	Dwarf bamboo grassland (%)	Recent clearcuts (%)	Pasture (%)	Natural outcrop (%)
Oboppu	23.7	64.0	5.8	0.7	0.7	1.3	3.8
Tarumai	48.0	47.2	1.8	0.5	1.4	0.0	1.1
Betsubetsu	51.1	48.7	0.0	0.0	0.1	0.0	0.1
Syadai	57.2	41.4	0.0	0.0	0.4	0.0	1.0
Uyoro	33.4	66.1	0.0	0.3	0.2	0.0	0.0
Shikiu	61.8	31.4	0.5	5.1	0.1	0.0	1.1
Tobyu	43.8	54.4	0.0	0.3	1.5	0.0	0.0
Meppu	45.5	48.1	0.0	0.0	6.4	0.0	0.0

Note: Stream channel was not included because of the very small area.

Table 4.3. Foraging guild, abundance, and scores of canonical correspondence analysis for bird species in eight study drainage basins.

Species	Spring			Summer		
	Mean abundance†	Axis 1 score	Axis 2 score	Mean abundance†	Axis 1 score	Axis 2 score
Flycatchers						
Narcissus flycatcher (*Ficedula narcissina*)	0.15 ± 0.38	-0.50	-0.16	0.18 ± 0.40	-0.32	0.21
Blue-and-white flycatcher (*Cyanoptila cyanomelana*)	0.11 ± 0.35	-0.76	0.29	0.07 ± 0.25	-0.85	0.16
Sooty flycatcher (*Muscicapa sibirica*)				0.02 ± 0.22	1.31	-0.08
Brown flycatcher (*Muscicapa latirostris*)	0.03 ± 0.21	-0.04	0.12	0.01 ± 0.17	-1.37	0.16
Gleaners						
Oriental cuckoo (*Cuculus saturatus*)	0.09 ± 0.29	0.57	-0.23	0.10 ± 0.31	0.18	-0.44
Little cuckoo (*Cuculus poliocephalus*)				0.004 ± 0.061	1.14	-0.33
Gray wagtail (*Motacilla cinerea*)	0.03 ± 0.24	-1.20	1.66	0.01 ± 0.09	-1.02	1.24
White wagtail (*Motacilla alba*)	0.01 ± 0.09	-1.26	1.21			
Japanese wagtail (*Motacilla grandis*)				0.004 ± 0.061	-0.93	-0.24
Olive-backed pipit (*Anthus hodgsoni*)				0.01 ± 0.11	0.68	0.69
Brown-eared bulbul (*Hypsipetes amaurotis*)	0.23 ± 0.65	-0.25	0.57	0.43 ± 0.74	-0.59	0.51
Bull-headed shrike (*Lanius bucephalus*)	0.01 ± 0.09	-0.95	-0.40	0.04 ± 0.30	0.44	-0.51
Winter wren (*Troglodytes troglodytes*)	0.06 ± 0.24	-0.67	-0.24	0.05 ± 0.24	-0.15	-0.30
Japanese robin (*Erithacus akahige*)	0.25 ± 0.50	-0.25	-0.51	0.28 ± 0.53	-0.04	-0.58
Siberian blue robin (*Erithacus cyane*)	0.22 ± 0.49	0.19	-0.22	0.14 ± 0.38	0.09	-0.13
Siberian bluechat (*Tarsiger cyanurus*)	0.01 ± 0.09	-0.68	1.11			
Siberian thrush (*Turdus sibiricus*)	0.01 ± 0.12	-1.21	0.89	0.01 ± 0.12	2.08	1.41
White's ground thrush (*Turdus dauma*)	0.02 ± 0.14	-0.59	-0.16	0.04 ± 0.24	0.09	0.40
Gray thrush (*Turdus cardis*)	0.12 ± 0.36	-0.37	0.81	0.17 ± 0.40	-0.31	0.73
Brown thrush (*Turdus chrysolaus*)	0.05 ± 0.26	-0.26	-0.29	0.14 ± 0.43	0.76	0.71
Short-tailed bush warbler (*Cettia squameiceps*)	0.41 ± 0.62	-0.03	0.32	0.36 ± 0.60	-0.01	0.12
Bush warbler (*Cettia diphone*)	0.90 ± 0.84	0.00	-0.31	0.86 ± 0.78	-0.07	-0.24
Arctic warbler (*Phylloscopus borealis*)	0.01 ± 0.12	-0.28	-0.25	0.004 ± 0.061	0.83	0.18
Pale-legged willow warbler (*Phylloscopus tenellipes*)	0.63 ± 0.82	-0.23	0.04	0.61 ± 0.65	-0.14	-0.13
Crowned willow warbler (*Phylloscopus occipitalis*)	0.54 ± 0.82	-0.33	-0.19	0.44 ± 0.62	-0.36	-0.08
Goldcrest (*Regulus regulus*)	0.07 ± 0.30	1.38	0.65	0.12 ± 0.42	1.32	0.43
Long-tailed tit (*Aegithalos caudatus*)	0.12 ± 0.47	-0.32	-0.24	0.08 ± 0.37	0.00	-0.19
Marsh tit (*Parus palustris*)	0.31 ± 0.68	-0.02	0.05	0.44 ± 1.00	0.16	0.02
Coal tit (*Parus ater*)	0.61 ± 0.82	0.60	0.10	1.47 ± 4.54	0.67	0.13
Varied tit (*Parus varius*)				0.01 ± 0.17	0.06	1.95
Great tit (*Parus major*)	0.28 ± 0.62	-0.28	0.19	0.20 ± 0.65	-0.17	-0.17
Japanese white-eye (*Zosterops japonica*)	0.03 ± 0.24	-1.16	-0.34	0.02 ± 0.16	0.02	0.17
Eurasian jay (*Garrulus glandarius*)	0.16 ± 0.41	0.19	0.40	0.11 ± 0.46	0.99	0.46
Carrion crow (*Corvus corone*)				0.01 ± 0.09	-0.38	1.05
Jungle crow (*Corvus macrorhynchos*)	0.01 ± 0.12	0.34	1.76			
Bark probers						
Great spotted woodpecker (*Dendrocopos major*)	0.06 ± 0.25	0.23	0.37	0.08 ± 0.31	-0.01	0.01
White-backed woodpecker (*Dendrocopos leucotos*)				0.01 ± 0.09	2.04	0.25
Pygmy woodpecker (*Dendrocopos kizuki*)	0.12 ± 0.37	-0.35	0.20	0.15 ± 0.42	-0.25	-0.24
Nuthatch (*Sitta europaea*)	0.04 ± 0.24	-0.14	0.16	0.10 ± 0.36	-0.22	-0.11
Tree creeper (*Certhia familiaris*)	0.004 ± 0.061	-1.00	0.80			

Table 4.3. Continued.

Species	Spring			Summer		
	Mean abundance†	Axis 1 score	Axis 2 score	Mean abundance†	Axis 1 score	Axis 2 score
Stream foragers						
Kingfisher (*Alcedo atthis*)				0.004 ± 0.061	-1.72	1.71
Brown dipper (*Cinclus pallasii*)	0.06 ± 0.27	-1.10	0.42	0.04 ± 0.21	-1.00	0.16
Herbivores						
Hazel grouse (*Tetrastes bonasia*)				0.01 ± 0.14	0.08	-1.67
Common pheasant (*Phasianus colchicus*)				0.004 ± 0.061	1.08	-1.62
Rufous turtle dove (*Streptopelia orientalis*)	0.16 ± 0.41	0.47	-0.25	0.19 ± 0.47	0.21	-0.20
Japanese green pigeon (*Sphenurus sieboldii*)	0.03 ± 0.16	0.52	0.83	0.04 ± 0.19	0.22	0.15
Black-faced bunting (*Emberiza spodocephala*)	1.14 ± 1.06	0.20	-0.02	1.43 ± 1.11	0.07	-0.01
Grey bunting (*Emberiza variabilis*)	0.04 ± 0.26	-0.35	0.24	0.03 ± 0.18	0.20	-0.62
Oriental greenfinch (*Carduelis sinica*)	0.004 ± 0.061	-0.98	0.04			
Bullfinch (*Pyrrhula pyrrhula*)	0.02 ± 0.16	-0.16	-1.04	0.10 ± 0.34	0.45	-0.93
Japanese grosbeak (*Eophona personata*)	0.16 ± 0.51	0.30	0.16	0.25 ± 0.57	-0.06	0.33
Hawfinch (*Coccothraustes coccothraustes*)	0.02 ± 0.19	-0.62	-0.37	0.03 ± 0.24	-0.06	0.32
Nutcracker (*Nucifraga caryoctactes*)	0.004 ± 0.061	1.68	0.94			
Raptors						
Black kite (*Milivus migrans*)	0.004 ± 0.061	-0.25	1.24			
Japanese lesser sparrow hawk (*Accipiter gularis*)				0.004 ± 0.061	0.45	0.27
Sparrow hawk (*Accipiter nisus*)				0.004 ± 0.061	0.45	-1.40
Hodgson's hawk eagle (*Spizaetus nipalensis*)				0.01 ± 0.12	-0.19	0.39
Ural owl (*Strix uralensis*)				0.004 ± 0.061	-0.82	-0.14

†Means ± SDs (birds/plot) determined by averaging abundance data from all study plots (0.8 ha, n = 269).

Table 4.4. Descriptions of environmental variables for local habitat, landscape position, and landscape composition in the 269 bird census plots in eight study drainage basins.

Variable	Description
Local habitat variables	
FC 1	Foliage cover of vegetation layer > 10 m in height (%)
FC 2	Foliage cover of vegetation layer 5-10 m in height (%)
UC 1	Understory cover of vegetation layer 2.5-5 m in height (%)
UC 2	Understory cover of vegetation layer 0.5-2.5 m in height (%)
HER	Cover of herbaceous layer 0-0.5 m in height (%)
SNG	Number of standing dead trees > 5 cm dbh
Slope	Mean slope within 100 m of census plot (degree)
Landscape position variables	
Elevation	Mean elevation within 100 m of census plot (m)
DNS	Distance from census plot's center to the nearest stream (m)
DNDF	Distance from census plot's center to the nearest deciduous forest (m)
DNCF	Distance from census plot's center to the nearest coniferous forest (m)
DNAF	Distance from census plot's center to the nearest alpine forest (m)
DNNF	Distance from census plot's center to the nearest nonforest area that includes dwarf bamboo grassland, recent clearcuts, pasture and natural outcrop (m)
Landscape composition variables	
DF 250	Deciduous forest within 250 m of census plot (%)
CF 250	Coniferous forest within 250 m of census plot (%)
AF 250	Alpine forest within 250 m of census plot (%)
NF 250	Nonforest area within 250 m of census plot (%)
DF 500	Deciduous forest within 500 m of census plot (%)
CF 500	Coniferous forest within 500 m of census plot (%)
AF 500	Alpine forest within 500 m of census plot (%)
NF 500	Nonforest area within 500 m of census plot (%)
DF 1000	Deciduous forest within 1,000 m of census plot (%)
CF 1000	Coniferous forest within 1,000 m of census plot (%)
AF 1000	Alpine forest within 1,000 m of census plot (%)
NF 1000	Nonforest area within 1,000 m of census plot (%)

Table 4.5. Results of two-way ANOVA testing for the effects of the distance from stream and season on adult aquatic insects, terrestrial aerial insects, and terrestrial foliage invertebrates, collected in each of the four-line transects.

Transect		Distance from stream			Season			Distance by season		
Stream	Forest	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Abundance of adult aquatic insects										
Small stream	Deciduous	67.4	4, 40	< 0.001	0.1	1, 40	0.753	1.6	4, 40	0.184
	Coniferous	64.1	4, 40	< 0.001	4.4	1, 40	0.041	3.4	4, 40	0.018
Large stream	Deciduous	21.5	4, 40	< 0.001	2.6	1, 40	0.115	4.8	4, 40	0.003
	Coniferous	64.6	4, 40	< 0.001	0.4	1, 40	0.524	4.5	4, 40	0.004
Abundance of terrestrial aerial insects										
Small stream	Deciduous	2.0	4, 40	0.120	57.8	1, 40	< 0.001	0.6	4, 40	0.638
	Coniferous	3.8	4, 40	0.011	54.5	1, 40	< 0.001	6.0	4, 40	0.001
Large stream	Deciduous	2.3	4, 40	0.077	108.2	1, 40	< 0.001	2.5	4, 40	0.057
	Coniferous	1.9	4, 40	0.130	72.4	1, 40	< 0.001	0.6	4, 40	0.682
Biomass of terrestrial foliage invertebrates										
Small stream	Deciduous	2.7	4, 80	0.038	117.1	1, 80	< 0.001	0.4	4, 80	0.839
	Coniferous	1.5	4, 80	0.216	312.4	1, 80	< 0.001	0.9	4, 80	0.482
Large stream	Deciduous	0.6	4, 80	0.699	169.6	1, 80	< 0.001	2.1	4, 80	0.093
	Coniferous	1.0	4, 80	0.399	162.4	1, 80	< 0.001	0.4	4, 80	0.834

Table 4.6. Results of stepwise multiple regression analysis for bird abundance (birds/plot) in spring and summer periods in the 269 bird census plots of eight study drainage basins.

Guild	Independent variable	Regression coefficient	Standard regression coefficient	Model R^2	Model F	Model P
Spring						
Flycatchers	DNS	-0.07	-0.33	0.25	28.9	< 0.001
	DNDF	-0.05	-0.32			
	FC 1	0.24	0.16			
Gleaners	DNS	-0.17	-0.44	0.47	57.8	< 0.001
	DNDF	-0.09	-0.32			
	Elevation	-0.15	-0.14			
	UC 2	0.27	0.12			
Bark probers	Elevation	-0.08	-0.16	0.05	7.4	< 0.001
	DNDF	-0.02	-0.15			
Herbivores	DNS	-0.07	-0.22	0.10	14.1	< 0.001
	DNDF	-0.04	-0.17			
All birds	DNS	-0.16	-0.43	0.46	57.0	< 0.001
	DNDF	-0.09	-0.34			
	Elevation	-0.15	-0.14			
	UC 2	0.23	0.10			
Summer						
Flycatchers	DNDF	-0.03	-0.23	0.08	12.1	< 0.001
	DNS	-0.03	-0.13			
Gleaners	DNS	-0.06	-0.23	0.17	13.4	< 0.001
	DNDF	-0.03	-0.18			
	HER	0.25	0.15			
	Slope	0.08	0.14			
Bark probers				0.00		
Herbivores	HER	0.47	0.24	0.06	16.5	< 0.001
All birds	DNS	-0.06	-0.26	0.20	21.8	< 0.001
	HER	0.37	0.24			
	DNDF	-0.03	-0.16			

Notes: See Table 4.4 for the legends of abbreviations. No significant model obtained for bark probers in summer period.

Table 4.7. Pearson product moment correlation coefficients with *P* values between mean bird abundance within drainage basin (calculated as habitat-weighted average of bird abundance within each drainage basin) and basin properties (n = 8 for all).

	Spring		Summer	
Variable	*r*	*P*	*r*	*P*
Mean elevation	0.28	0.516	0.35	0.408
Basin slope	0.31	0.471	0.51	0.206
Relative relief	-0.08	0.859	0.10	0.830
Drainage density	0.76	0.026	0.71	0.050
Drainage frequency	0.33	0.446	0.24	0.577
Bifurcation ratio	0.48	0.241	0.56	0.158
% deciduous forest	0.47	0.254	0.55	0.166
% coniferous forest	-0.41	0.334	-0.35	0.409
% alpine forest	-0.34	0.434	-0.61	0.110
% nonforest area†	-0.24	0.578	-0.57	0.147

†Includes dwarf bamboo grassland, recent clearcuts, pasture, and natural outcrop.

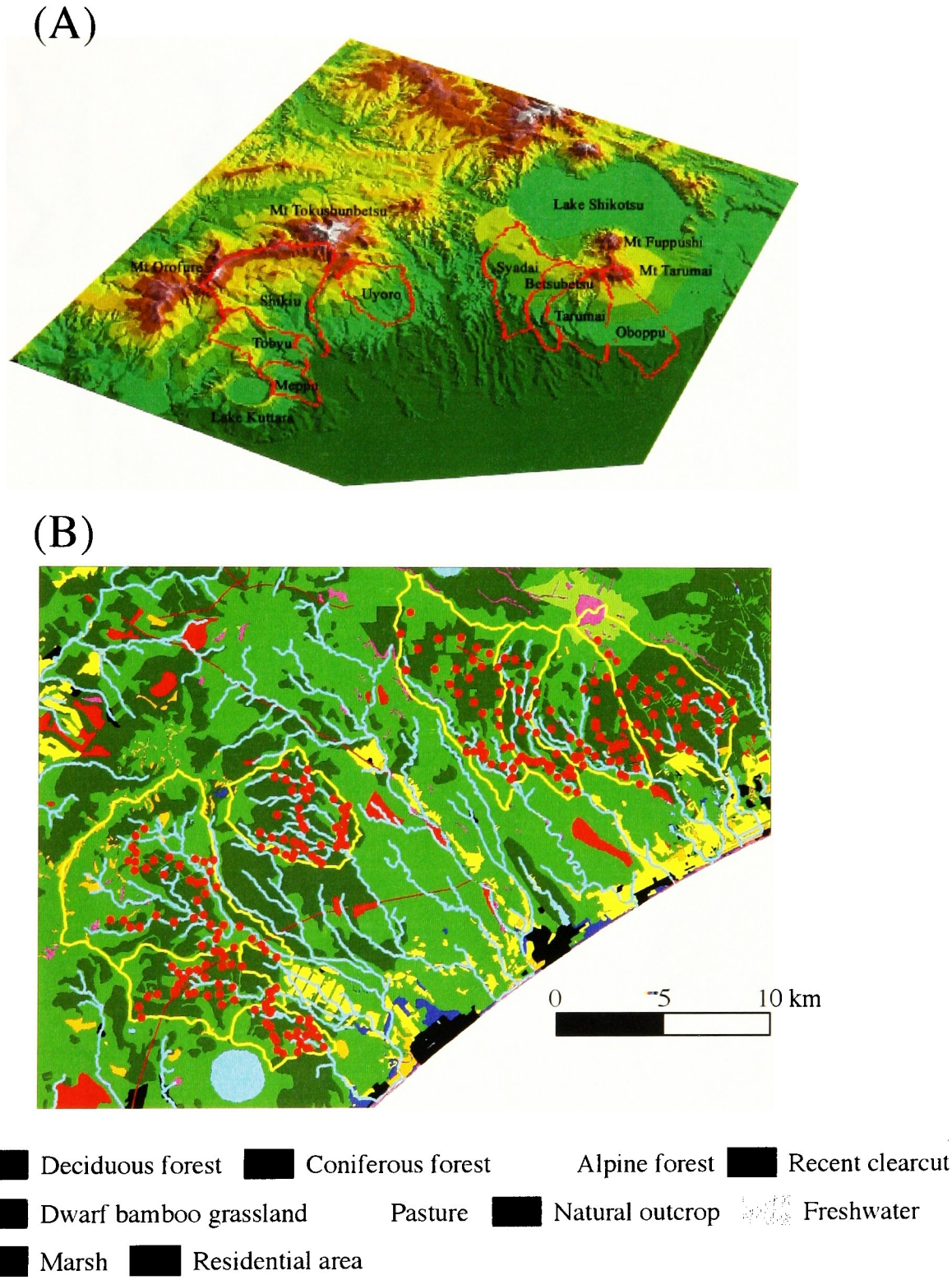


Fig.4.1. Location of the eight study drainage basins in southwestern Hokkaido, Japan (A) and general landscape classes of the study area (B). Red circles indicate bird census plots.

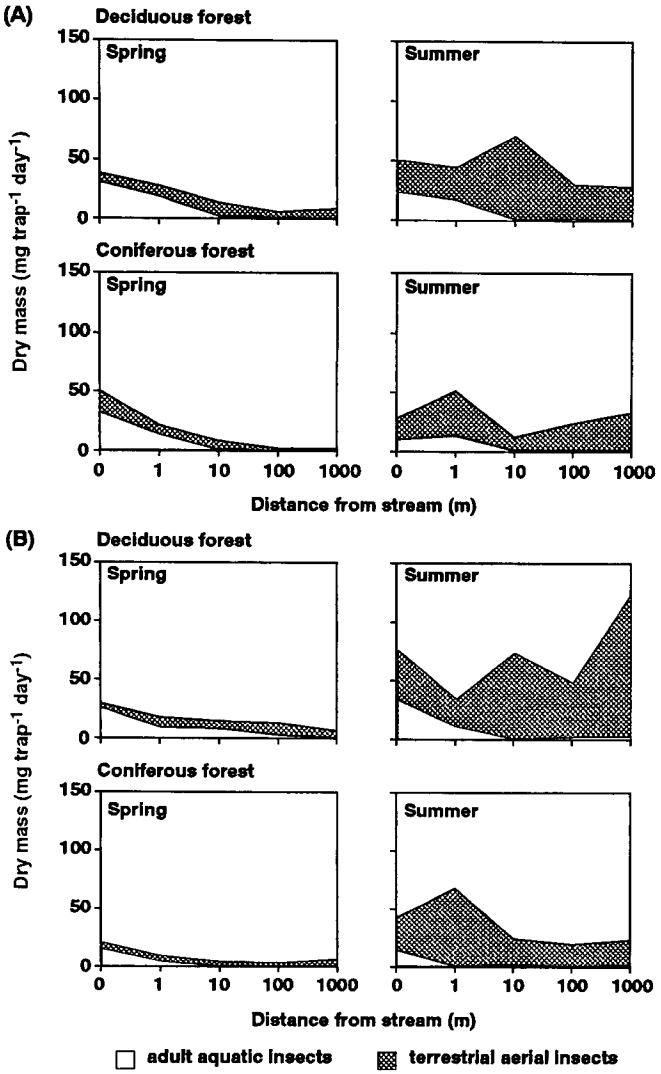


Fig. 4.2. Average abundance of aquatic and terrestrial aerial insects, collected at different distances from stream channels, in spring and summer periods in deciduous and coniferous forests. (A) Insect abundance collected along the transect established for small streams (< 10 m wetted width), and (B) for large streams (≥ 10 m wetted width).

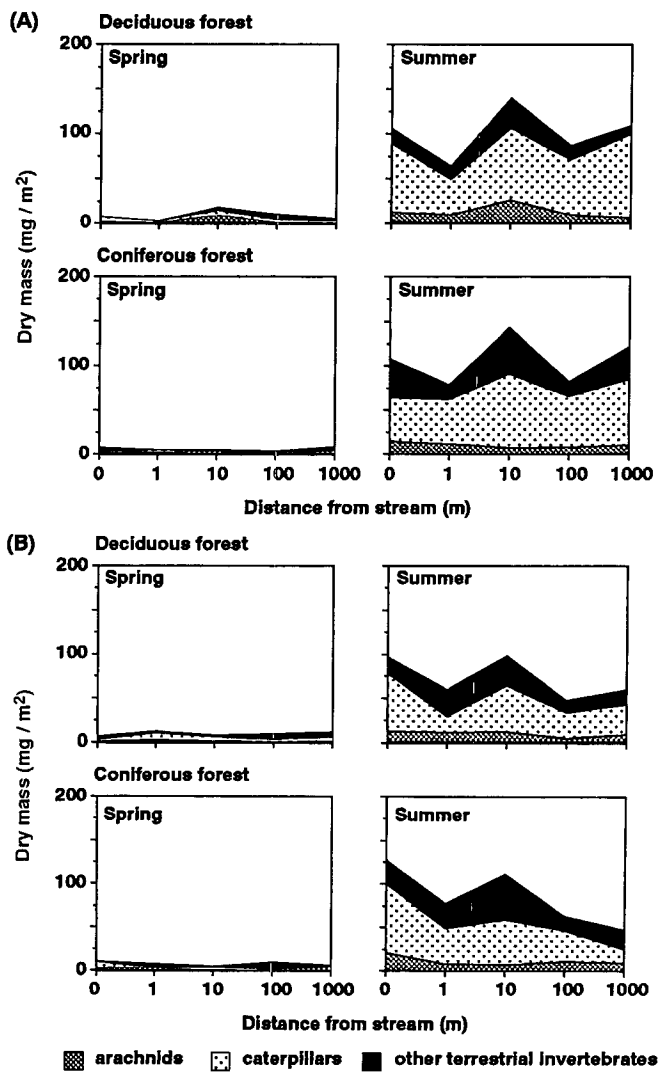


Fig. 4.3. Average biomass of foliage invertebrates, collected at different distances from stream channels, in spring and summer periods in deciduous and coniferous forests. (A) Invertebrate biomass collected along the transect established for small streams (< 10 m wetted width), and (B) for large streams (≥ 10 m wetted width).

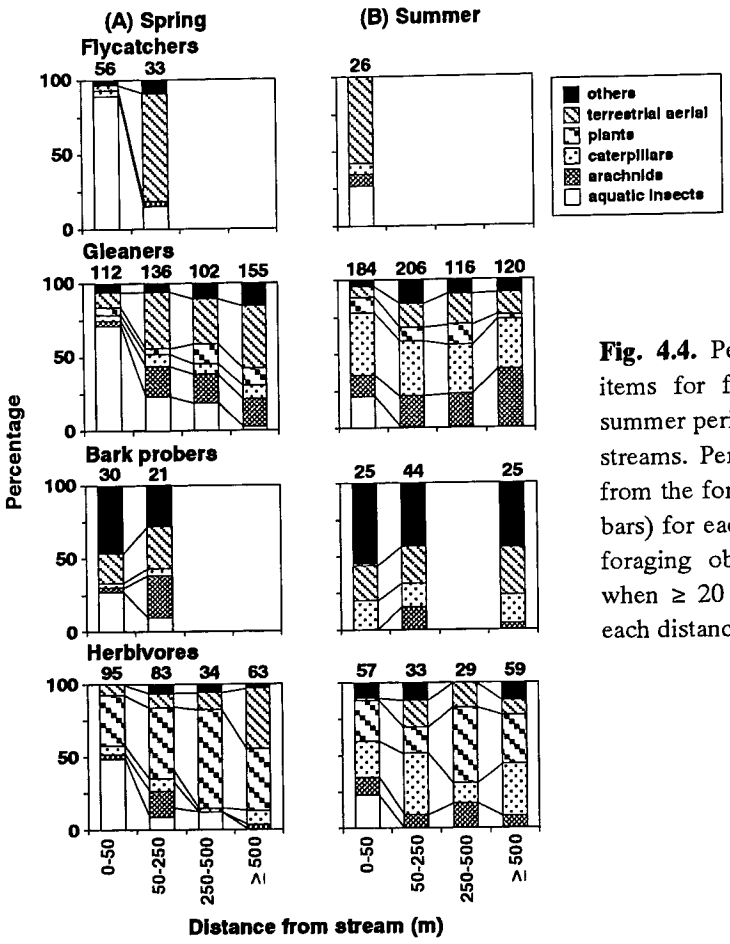


Fig. 4.4. Percentage composition of prey items for foraging guilds in spring and summer periods at different distances from streams. Percentage values were estimated from the foraging frequency (figures above bars) for each prey item recorded by direct foraging observations. Data were shown when ≥ 20 prey items were identified for each distance category.

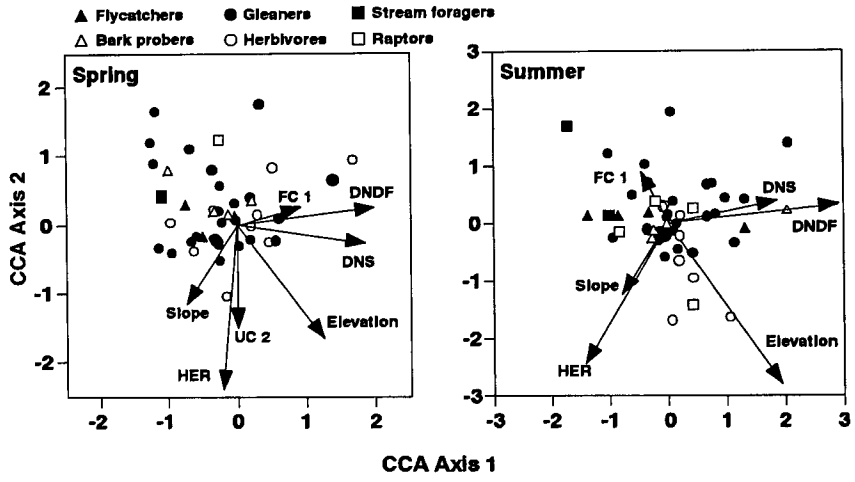


Fig. 4.5. Canonical correspondence analysis (CCA) ordination plot showing species distributions in relation to environmental variables for spring and summer periods. Each symbol represents an individual species (see Table 4.3). The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along the particular environmental gradient. Labeled arrows indicate the direction along which each environmental variable changes most. See Table 4.4 for the legends of abbreviations for environmental variables. Average values for environmental variables are found at the origin of the arrows, and the numerical value of an environmental variable increases from the origin toward the tip of the arrow corresponding to that variable. The arrow denoting UC 1 in summer period was not shown because of its very short length.

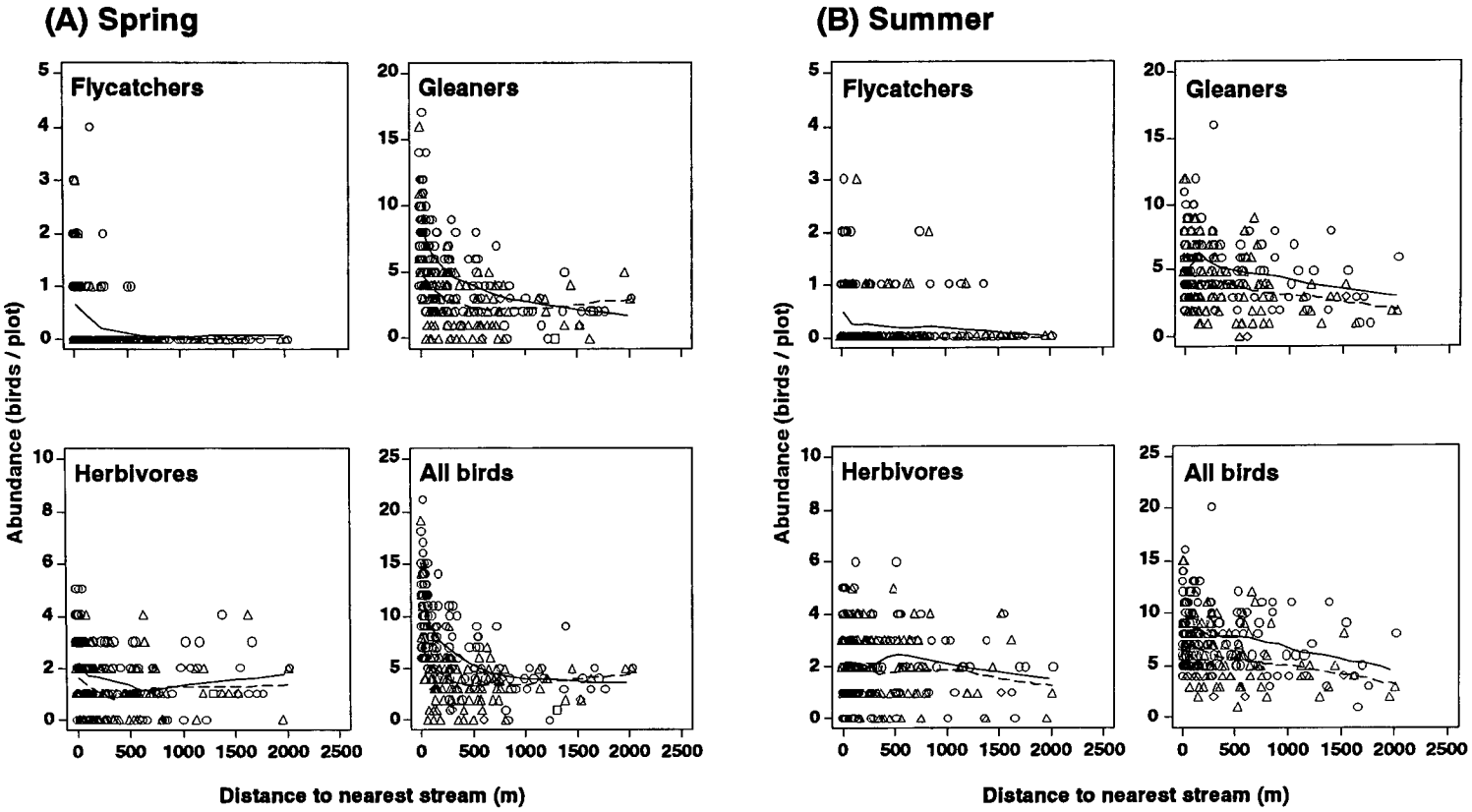


Fig. 4.6. Abundance of flycatchers, gleaners, herbivores and all birds, in relation to the distance to the nearest stream, in (A) spring and (B) summer periods. Each data point is for one bird census plot. Solid and broken lines in data field are LOWESS regression curves for the plots located in deciduous and coniferous forests, respectively. Circles, deciduous forest; triangles, coniferous forest; squares, alpine forest; diamonds, nonforest area.

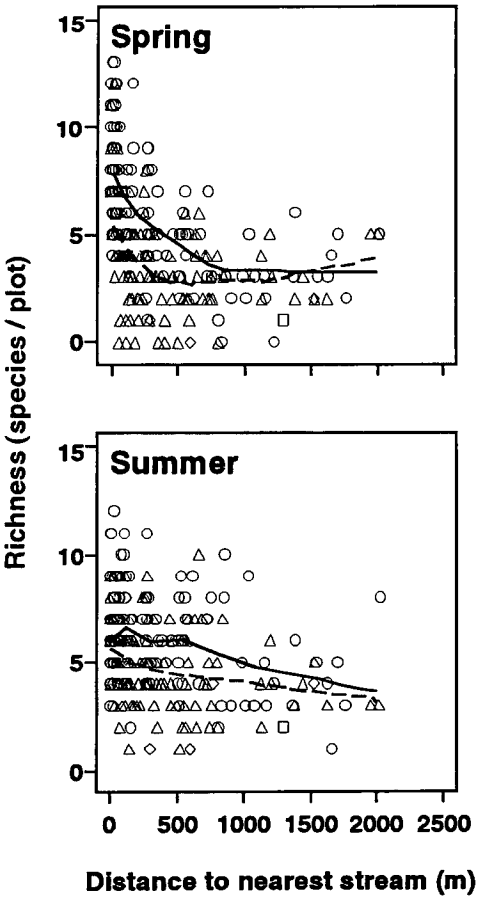


Fig. 4.7. Species richness in relation to the distance to the nearest stream, in both spring and summer periods. See Fig. 4.6 for figure legends.

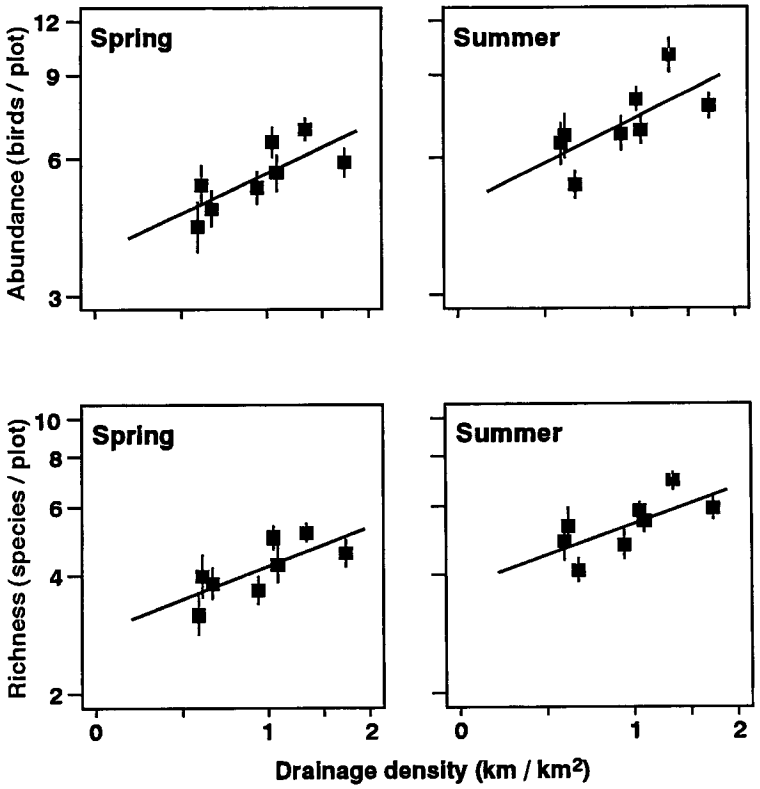


Fig. 4.8. Relationships between drainage density and both mean bird abundance and species richness of drainage basins in spring and summer periods. Each data point is for one drainage basin. Mean abundance and richness within each drainage basin were calculated as habitat-weighted average of both parameters within each drainage basin (see text for detail). Standard error (± 1 SE) for each value and regression lines shown. All axes given as logarithmic scales.

CHAPTER 5
GENERAL DISCUSSION

This study showed that fluvial geomorphology exerts powerful, even dominant, influences over the adjacent terrestrial predator populations in highly seasonal landscapes. Stream geomorphic features interact with the traits of aquatic insects (e.g., life history, feeding types and mobility) to produce spatial heterogeneity of aquatic prey transfer, which is often responsible for the distribution of riparian generalist predators in temperate forested basins. Here I summarize the results obtained at three spatial scales (channel geomorphic unit, stream reach, and drainage network) within the drainage basin system.

First, at the channel unit scale, I examined the effects of pool-riffle structure on aquatic insect emergence and the distribution of riparian web-building spiders. Pools with slow water stored greater amounts of terrestrial detritus than riffles, allowing more abundant detritivorous insects to develop in pools. The greater detritivore biomass in pools resulted in an emergence rate of aquatic insects from pools ~ 4-5 times greater than that from riffles. In the riparian forest, web-building spiders (Tetragnathidae and Linyphiidae) were distributed in accord with the emergence rates of aquatic detritivores, upon which both spider groups heavily depended. Consequently, pools supported two times the density of tetragnathid spiders in streamside habitats than did riffles. These findings suggest that in headwater ecosystems, spatial elements that control the storage of organic materials in flowing water (e.g., pools or woody debris) play a significant role in determining the strength of forest-stream linkages at the channel unit scale.

Second, at the stream reach scale, I examined the effects of stream meanders on the abundances of adult aquatic insects and insectivorous birds in riparian forests. In spring, flycatchers and gleaners concentrated their foraging attacks around the stream channel, preying intensely upon emerging aquatic insects. The riparian forests including highly sinuous streams had greater aquatic insect abundance, because stream meanders increased the amount of both stream edge and stream surface, where emerging aquatic insects readily penetrate. Consequently, stream meanders elevated flycatcher and gleaner abundances by facilitating the energy transfer from stream production to these predators. These results suggest that the boundary shape,

delimited by stream channel, is a spatial feature that strongly affects the degree of trophic connectivity between forest and stream.

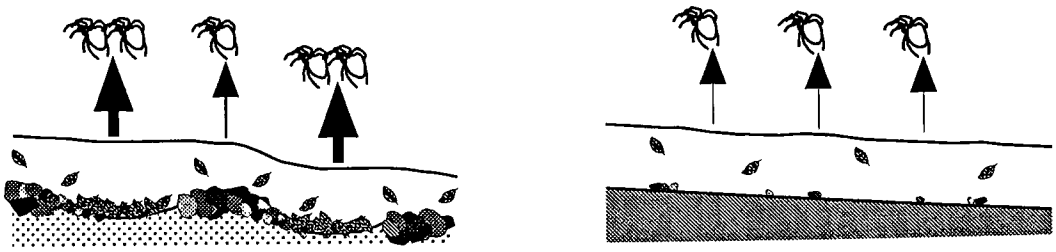
Third, at the drainage basin scale, I examined the effects of stream network structure on the distribution and abundance of forest birds in temperate forested basins. In spring when terrestrial prey abundance is depleted, many insectivorous birds tended to occur in habitats located in close proximity to streams and preyed intensely upon emerging aquatic insects. Although birds ceased to aggregate around streams in summer as terrestrial prey became plentiful, the abundance and diversity of bird assemblages were the highest at the junction of forests and streams in the drainage basins. Such 'stream effect' on birds spread over the whole basin scale; drainage basins with longer stream channels per unit area had higher bird abundance and species diversity. Moreover, such effects continued from spring through summer. These results indicated that despite the relatively small areas, drainage network structure is the most important landscape element that supports diverse and abundant avifauna, at least in part, by controlling the energy transfer from stream to forest ecosystems.

Supported by these findings, I can conclude that stream habitat structure plays disproportionately large roles in determining the density and diversity of terrestrial predators at any scale of hierarchical components contained within the drainage basin. My results have implications for understanding how watershed disturbances by human activities influence terrestrial predators. Hydrological alterations, such as channelization, are now recognized as a major cause of the impoverishment of stream biodiversity (Pringle et al. 2000, Rosenberg et al. 2000). The present results predicted that such river modifications will also influence terrestrial predator populations. For instance, in many regions, pool-riffle structures have decreased owing to channel alterations, sedimentation and the loss of pool-forming elements such as the decrease in large woody debris resulting from riparian timber harvest (Inoue and Nakano 1998, McIntosh et al. 2000). Since pools serve as an important habitat for many stream fishes, effects of reduced pool habitats on lotic fish communities have been of great interest to stream ecologists. In addition to that, changes in pool-riffle structure should also have dramatic effects on organic matter flow, an aspect that should not go unheeded (Fig. 5.1). In the absence of retention devices a stream functions much more like a pipe, with organic materials being rapidly flushed from the system (Bilby and Likens 1980, Minshall et al. 1983). This leads to a prediction that the loss of pool habitats will impoverish detrital-based benthic communities and will even exert marked

influences over populations of riparian web-building spiders by reducing the flux rate of stream production to the neighboring forests (Fig. 5.1).

The effects of anthropogenic watershed disturbances on the maintenance of terrestrial communities can be predicted even at the spatial scales of stream reach and drainage network. The present results predict that species diversity and populations of forest bird assemblages may be susceptible to the intensive hydraulic alterations, such as short cutting and straightening of stream channels and the drying out of streams by water abstraction or damming (Fig. 5.1) (Pringle et al. 2000, Rosenberg et al. 2000). Moreover, streamside disturbances that depress the aquatic insect communities over an extensive area of streams, such as heavy sedimentation resulting from riparian deforestation (Harding et al. 1998, Iwata et al. 2003), might accelerate the impoverishment of bird assemblages by reducing the aquatic prey flux from streams. To date, retention and/or restoration of both riparian buffer strips and unfragmented forests have been encouraged as the vital strategies for maintaining forest bird communities (Andrén 1994, Knopf and Samson 1994, Brooks et al. 1999, Drapeau et al. 2000). These management practices have proceeded with great concern over the rapidly changing land-use regime in the terrestrial ecosystems. However, importance of riverine landscapes to the maintenance of terrestrial communities has rarely been taken into consideration. I propose that considerable emphasis should be placed more on the landscape-based management approach that considers both stream and forest ecosystems in conjunction, for watershed biodiversity conservation.

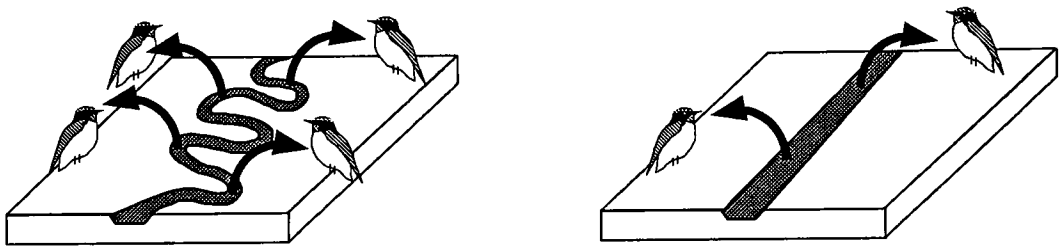
(A) Channel geomorphic unit



Unregulated Regulated

Loss of pool-riffle sequences

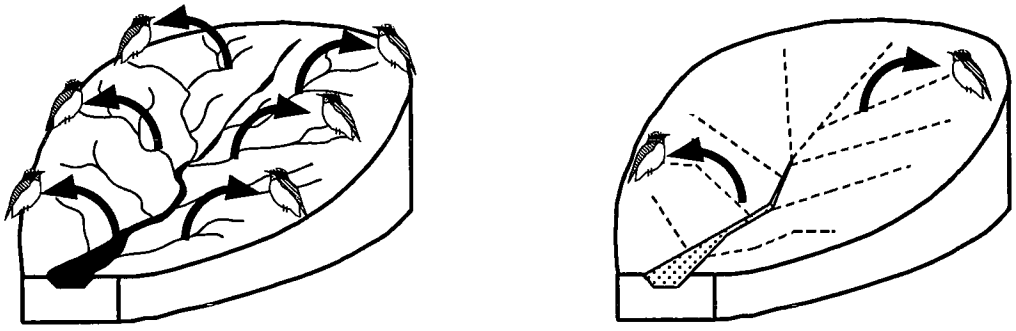
(B) Stream reach



Unregulated Regulated

Straightening of meandering channels

(C) Drainage basin



Unregulated Regulated

Modification of drainage networks

Fig. 5.1 Possible impacts of hydraulic alterations on terrestrial predator populations by altering the magnitude of aquatic prey transfer from stream to forest ecosystems. Arrows indicate energy flow from streams to terrestrial predators via aquatic insect emergence. 'Regulated' streams mean streams serving watersheds on which manmade controls or devices are present.

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要旨

The roles of fluvial geomorphology in the trophic flow from stream to forest ecosystems
(河川から森林への栄養移流における河川地形の役割)

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河川地形が羽化水生昆虫を採餌する陸上捕食者の分布と個体数に及ぼす影響を調べた．調査は河川形態の代表的な3つの階層区分（流路単位，河道区間，流域）を対象に，北海道南西部の森林流域で実施した．流路単位スケールでは，瀬と淵の繰り返し構造が造網性クモ類の分布に及ぼす影響を明らかにした．低流速により粒状有機物が多く貯留される淵では，それらを餌資源とする水生昆虫の生物量が瀬より有意に大きかった．また，淵からの水生昆虫羽化量は瀬の 4-5 倍に達し，これによって淵は河畔域のアシナガグモ類を高い個体群レベルに維持することを示した．河道区間スケールでは，川の蛇行が河畔林の昆虫食性鳥類の個体数に及ぼす影響を明らかにした．蛇行は川と森の隣接域を増加させることで河畔林内の羽化水生昆虫量を増加させること，またそれらを多く採餌する空中採餌型および啄み採餌型鳥類の個体数を増加させることを示した．流域スケールでは，水路網の発達が鳥類群集の分布と個体数に及ぼす影響を調べた．陸上資源の乏しい春期には，多くの鳥類は河川周辺に集中分布し羽化水生昆虫を多く採餌していた．このような鳥類の河川への強い依存は，流域全体の鳥類個体数にも影響を及ぼしていた．すなわち水系密度の高い流域ほど鳥類の平均個体数が多く，その傾向は春だけでなく夏まで持続した．このことから，流域内の河川の空間配置は鳥類群集に強い影響を及ぼすことが示された．

本研究により，羽化水生昆虫の川から森への移流量は河川地形に依存すること，このため流域内のあらゆる階層区分において河川地形は陸上捕食者の分布と個体数に強い影響を及ぼすことを明らかにした．これらの知見をもとに，瀬-淵構造の喪失・河道の直線化などの河川改修や利水による水路の干上がりは，水生生物のみならず陸上の生物群集にも強い影響を及ぼす可能性を指摘した．